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STUDIES IN ARTOCARPUS AND ALLIED GENERA,¹ I. GENERAL CONSIDERATIONS

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MEMBERS OF THE GENUS *Artocarpus* are the most commonly encountered representatives of the Moraceae in the lowland forest of the Old World tropics (Africa excepted) apart from the ubiquitous *Ficus*. The genus also includes two important food-plants, the Breadfruit (*A. incisus*) and the Jack (*A. heterophyllus*), which now have a circumtropical distribution as cultivated plants, owing to the efforts of man, which include, of course, the well-known voyage of Captain Bligh ending in the mutiny on the *Bounty*. The fruits of a number of other species are edible, some being planted for the sake of these, and many species provide valuable timber, although they do so in general as scattered members of the forest flora, for the only example of gregarious behaviour is that of *Artocarpus incisus* (probably little, if at all, modified from the original form) acting as a dominant member of the forests of the river-swamps of New Guinea.

The genus *Artocarpus* is singled out by its compound fruit or syncarpium, which attains a large size in some species, notably in the two cauliflorous species, the Jack and the Chempedak (*A. integer*, frequently cultivated in Malaysia). The structure of this fruit has been the subject of special attention in this study with the object of determining the differences between it and the syncarpous fruits of two other small genera of the same area and alliance, *Parartocarpus*, which has frequently been confused with *Artocarpus*, and *Hullettia*, which has proved, somewhat unexpectedly, to show a relationship with *Parartocarpus*, having previously been placed in a different subfamily of Moraceae. A third small genus, *Prainea*, which is more closely related to *Artocarpus* than either of these, although the female inflorescence is not a syncarpium, is also included. It provided another immediate problem, since details of the leaf anatomy had led an earlier author (Renner, 1907²) to unite *Prainea* with *Artocarpus*, necessitating a re-evaluation of his work and its extension to cover all the species here

¹ This series of papers is based on a thesis presented to the University of Cambridge, England, in July 1956 for the degree of Ph.D.

² The dates refer to the bibliography at the end of the paper.

recognized, from which it has been concluded that his action was not justified.

The four genera to be included in this study are thus *Artocarpus* J. R. & G. Forster, which is here recognized as consisting of about fifty species, *Prainea* King (four species), *Parartocarpus* Baillon (three species) and *Hullettia* King (two species). They are lactiferous trees or, less commonly, shrubs restricted in general to the lowland tropical evergreen forest of the Asiatic-Malaysian region although some species may extend to slightly higher altitudes or into areas of deciduous forest. A few of the latter are restricted to regions with a distinct dry season and are themselves either deciduous or evergreen, but the rest are merely tolerant of a short dry season, often adopting the deciduous habit when they grow in such a climate.

With an African genus, *Treculia* Decaisne ex Trécul, which has perhaps six species, they form a group within the Old World Moraceae characterized by condensed, capitate, unisexual inflorescences which is sufficiently distinct to justify independent study, although it cannot be entirely certain that it represents a natural assemblage of genera. These genera have been assigned to the subfamily Artocarpoideae tribe Artocarpeae and, as will be shown later, constitute the Old World members of this tribe. Although the three subfamilies of the Moraceae — Moroideae, Artocarpoideae and Conocephaloideae — which are distinguished by the position of the ovule and of the stamens in bud, may be valid groups if some exceptions are allowed for, it is not felt that the present classification of the Moraceae offers a sufficiently satisfactory basis for a detailed discussion of the position within the family of the genera being studied, and there will be given only a brief review of Bentham and Hooker's classification of the Artocarpeae. Full revisions of *Prainea*, *Artocarpus*, *Parartocarpus* and *Hullettia* will be given, in this order, in subsequent papers, while in this introductory paper the more general problems of the generic distinctions will be considered.

The genus *Artocarpus* was described by J. R. & G. Forster in 1776 and has been monographed as a whole once before in 1847 by Trécul, who established two subgenera, *Jaca* and *Pseudojaca*, which are here maintained (the former as subg. *Artocarpus*), on the basis of "alternate" (i.e., spiral) *vs.* distichous arrangement of the leaves and amplexicaul *vs.* non-amplexicaul stipules, as well as on a character of the male flowers which later proved untenable. *Parartocarpus* was described by Baillon in 1875, but was not very clearly distinguished by him from *Artocarpus*, and when King monographed the species of *Artocarpus* in India and the Malay Peninsula in 1889, he included unawares two species of *Parartocarpus*, the discordant characters of which led him to reject Trécul's subgenera. King had also described *Prainea* and *Hullettia* in 1888 but, mistaking the position of the ovule, he assigned them to the Conocephaloideae. In 1902 Beccari published an account entitled "Nuove specie di *Artocarpeae* Malesi e Papuane" in which he pointed out the affinity between *Prainea* and *Artocarpus* and briefly commented on the differences between the latter and

Parartocarpus. The final paper of major importance in the classification of the genera is Renner's study of the leaf anatomy of the Moraceae: Artocarpoideae and Conocephaloideae, published in 1907. Renner re-established Trécul's subgenera but treated them, together with *Prainea*, as three sections under *Artocarpus*, a proceeding which might be justifiable on the basis of leaf anatomy alone, but not if the inflorescence structure is also taken into account.

Various observations had thus been made on the differences between *Artocarpus*, *Prainea* and *Parartocarpus*, but the status and distinguishing characters of the genera had not been fully elucidated, nor had the true affinities of *Hullettia* previously been noted. Although the inflorescence structure of these genera is complex and its morphological derivation is not immediately apparent, no study of the development had been made, apart from a few superficial observations published by Baillon in 1863.

In this introductory paper the results of studies carried out in the course of this revision on the morphology and development of the inflorescences are described and their significance is discussed. Other characters that have been found to be of importance at the generic level, namely, seed structure and germination, shoot morphology and leaf anatomy are then considered. Reference is made as necessary to the work of earlier authors, but fuller historical accounts will be found under each genus. Before entering on the more detailed discussions a summary follows of the characters of these four genera, with their resemblances and differences as established in this survey, and a brief review of their position within the Moraceae.

The genera included in this study have condensed, unisexual, usually many-flowered, axillary inflorescences. (In *Parartocarpus* occasional abnormal inflorescences are bisexual.) The flowers are sessile upon or sunken into a pulvinate, globose, or cylindric, fleshy receptacle bearing interfloral (*Prainea* and *Artocarpus*) or involucral (*Parartocarpus* and *Hullettia*) bracts, the (upper) surface of the receptacle being completely covered. They have no rudiments of the organs of the opposite sex. The stamens or ovaries are enclosed in tubular or 2-4-lobed or -partite perianths (*Prainea* and *Artocarpus*) which may fuse partially or completely to form a syncarpium (*Artocarpus*), or they are sunken in cavities in the receptacle (*Parartocarpus* and *Hullettia*). If the latter, the anthers or styles are exerted either between indurated processes covering the surface and (?) representing perianths (*Parartocarpus*), or through simple perforations in the naked receptacle (*Hullettia*). The male flower has one (*Prainea* and *Artocarpus*), two (*Hullettia*) or up to three (*Parartocarpus*) stamens, which are erect in bud, and the female flower has a unilocular ovary with a pendulous ovule and a simple or bifid style. The seeds and embryos are large with little or no endosperm and no period of dormancy. The embryo has either equal or unequal, appressed cotyledons, and is straight (*Prainea*, *Artocarpus* and *Hullettia*) or curved, the cotyledons being folded just above the base and incumbent (*Parartocarpus*). Germination (otherwise unknown) is hypogeal in *Artocarpus* and epigeal in *Parartocarpus*. The leaves are penninerved (except in *Artocarpus altissimus*) with microscopic epi-

dermal gland-hairs providing characters of taxonomic value and (in *Prainea* and *Artocarpus* subg. *Artocarpus*) resin-containing cells in the mesophyll. They are spirally (*Artocarpus* subg. *Artocarpus*, *Parartocarpus* and *Hullettia*) or alternately and distichously (*Prainea* and *Artocarpus* subg. *Pseudojaca*) arranged with paired or (in *Parartocarpus*) single stipules enclosing the terminal bud (amplexicaul in *Artocarpus* subg. *Artocarpus*, acicular in *Hullettia*).

From this brief account the more important distinguishing characters of the genera may be derived. In *Prainea* and *Artocarpus* the stamens and ovaries are enclosed by perianths, usually mixed with interfloral bracts, and a clearly differentiated involucre is lacking. The embryo is straight, or nearly so, and in *Artocarpus* germination is hypogeal, with no elongation of the hypocotyl. The primary difference between the genera is that in *Prainea* the perianths in the female inflorescence remain free, but in *Artocarpus* they are fused with each other to form a syncarpium, though the fusion usually occurs only in the superficial layer, leaving the perianths free at the level of the ovary. The subgenera of *Artocarpus* can be distinguished from each other and from *Prainea* by the characters of the shoot. In *Artocarpus* subg. *Artocarpus* the leaves are spirally arranged on the shoot with large amplexicaul stipules leaving annulate scars, while in subg. *Pseudojaca* and *Prainea* they are alternate and distichous with small lateral stipules; but the epidermal gland-hairs of *Prainea* and *Artocarpus* subg. *Artocarpus* have multicellular heads and the mesophyll contains resin-cells, while in *Artocarpus* subg. *Pseudojaca* the heads of the gland-hairs are usually unicellular and the mesophyll lacks resin-cells.

In *Parartocarpus* and *Hullettia* the stamens and ovaries are enclosed in cavities of the receptacle, the walls of which have been shown in the former to be intercalary in origin, and there is a well developed involucre of bracts which are basal in *Parartocarpus* and vary to an equatorial position in *Hullettia*. In *Parartocarpus* the embryo is curved, having the appressed cotyledons folded just above the base and incumbent, and germination is epigeal, the hypocotyl elongating markedly and carrying the cotyledons well above the ground, where they separate and become green. In this genus the surface of the inflorescence is armoured from indurated processes some of which are fused basally around the openings to the cavities in the receptacle. This suggests that they represent perianth segments, but their similarity to the interfloral bracts of the allied but less reduced African genus *Treculia* indicates that they may be derived from the latter. In *Hullettia* the fleshy receptacle is naked and both perianths and interfloral bracts appear to be completely absent. The shoot has spirally arranged leaves in both genera, but in *Parartocarpus* each leaf has a single triangular, intrapetiolar, non-amplexicaul stipule (distinguishing the genus from species of *Artocarpus* subg. *Artocarpus* in which the syncarpium is superficially similar), whereas in *Hullettia* the stipules are paired, lateral and acicular.

Within the subfamily Artocarpoideae of the Moraceae, which is characterized by the erect position of the stamens in bud and the pendulous

ovule (compared with incurved stamens in the Moroideae and the erect ovule of the Conocephaloideae), these four genera, together with *Treculia*, represent the Old World members of the tribe Euartocarpeae of Benthams and Hooker (now to be written as Artocarpeae).³ These authors also included *Cudrania*, which should have been assigned to the Moroideae and will not be considered further, and *Balanostreblus*, which has been shown (Jarrett, 1958) to be based on a species of the South American genus *Sorocea* introduced into the Botanic Garden, Calcutta.

The classification of the Moraceae is still fundamentally that of Benthams and Hooker (1880) and it may be in some need of revision, since the New World genera of the Artocarpeae do not appear to be closely related to those of the Old World. However, the latter form a fairly well-defined group, characterized by capitate, many-flowered inflorescences in which the flowers completely cover the surface of the receptacle (i.e., without the naked strips found in some American genera), and in which there were probably originally both interfloral bracts and a basal involucre. *Treculia*, which is the least reduced genus, is the only one to have both interfloral and involucre bracts well developed, as well as perianths enclosing stamens and ovaries. There is also a rudiment of the ovary in the male flower. It is allied with *Parartocarpus* by the presence of an involucre and the orientation of the embryo. Nevertheless, it must be realized that there is nothing except general similarity to justify the classification of *Prainea* and *Artocarpus* with *Treculia*, *Parartocarpus* and *Hullettia*; the superficial resemblance of the syncarp in *Artocarpus* and *Parartocarpus* is due to parallel evolution.

The study of this group was suggested to me by Mr. E. J. H. Corner, and was carried out under his guidance at the Botany School, Cambridge, England. I should like to record my grateful appreciation of Mr. Corner's continued and stimulating interest in the research and I am further indebted to him for the use of his notes made in Malaya on field characters and details of seed structure and germination. In addition, numerous specimens of inflorescences preserved in alcohol, which had been collected by him, were loaned for study from the Botanic Gardens, Singapore. These, together with preserved material sent from Kebun Raya, Bogor, Indonesia, and by Mr. T. B. Worthington, Peradeniya, Ceylon, and Mr. G. R. Proctor, Science Museum, the Institute of Jamaica, Kingston, Jamaica, were of great value in studying the structure of the inflorescences. Mr. Chew Wee Lek, now at the Botany School, Cambridge, also generously made available to me inflorescences and young seedlings of *Treculia africana* Decaisne ex Trécul preserved in alcohol which he had collected in Singapore. Seeds of various species of *Artocarpus* were kindly sent for germination by the director of the Botanic Gardens, Singapore.

³ Actually *subtribe* Euartocarpeae of *tribe* Artocarpeae of Benthams and Hooker, but the ranks and suffixes of these subdivisions have been altered to accord with the modern practice of treating their "Urticaceae" as consisting of the Ulmaceae, Moraceae, Cannabinaceae and Urticaceae (s.s.).

The material which has been examined in the course of this revision is that in the following herbaria:

- Arnold Arboretum, Harvard University, Cambridge, Mass. (A)
- British Museum (Natural History), London, England. (BM)
- Herbarium Bogoriense, Bogor, Java, Indonesia. (BO)
- Botanical Museum and Herbarium, Copenhagen, Denmark. (C)
- Indian Botanic Garden, Calcutta, India. (CAL)
- Botany School, University of Cambridge, England. (CGE)
- Forest Research Institute and Colleges, Dehra Dun, India. (DD)
- Herbarium Universitatis Florentinae, Firenze, Italy. (FI)
- Gray Herbarium, Harvard University, Cambridge, Mass. (GH)
- The Herbarium, Royal Botanic Gardens, Kew, England. (K)
- Rijksherbarium, Leiden, Netherlands. (L)
- New York Botanical Garden, New York. (NY)
- Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie, Paris. (P)
- Philippine National Herbarium, Manila, Philippines. (PNH)
- Sarawak Museum, Kuching, Sarawak. (SAR)
- Herbarium of the Botanic Gardens, Singapore. (SING)
- Botanical Museum and Herbarium, Utrecht, Netherlands. (U)
- U. S. National Museum (Department of Botany), Smithsonian Institution, Washington, D. C. (US)

Thanks are due to the directors and staffs of these institutions for the loan of material and also for hospitality at the British Museum (Natural History), The Herbarium, Kew, the Rijksherbarium, Leiden, the Muséum d'Histoire Naturelle, Paris, and the Botanical Museum and Herbarium, Utrecht.

The work on which this revision is based was carried out during the tenure of a Maintenance Grant from the Department of Scientific and Industrial Research, the Frank Smart Studentship for Research in Botany in the University of Cambridge, and a Caroline Turle Scholarship of Newnham College, Cambridge. A grant was also made by Newnham College toward the expenses of a visit to Leiden and Paris during March and April, 1955. Grateful acknowledgment is made for this support.

MORPHOLOGY AND DEVELOPMENT OF THE INFLORESCENCES

The morphology of the inflorescences in the genera under review has been studied by dissection and sectioning at anthesis and maturity and by examining different stages in the development where suitable material has been available. Material preserved in alcohol has been used as far as possible and has been supplemented by dried inflorescences, expanded by boiling in water, which can be quite suitable for study if they have been dried quickly (being sliced if they are at all large) and protected from insect attack. The development has not been studied previously except for brief observations on cultivated species of *Artocarpus* published by Baillon (1863) and Subba Rao (1940), which will be commented on below.

The arrangement of the inflorescence in the Urticaceae and Moraceae has been established as basically cymose by Bernbeck (1932) who showed that the dorsiventral inflorescences found in this alliance originate in the suppression of apical growth in a mono- or dichasium, the appearance of the primordia of the flowers and their subtending bracts being delayed, so that they arise on a variously shaped cushion of tissue representing the compressed inflorescence axis, or receptacle. He was able to do this both by making comparative studies in one genus (e.g., *Urtica*) showing progressive reduction in the inflorescence, and by analysing the arrangement and order of origin of the primordia in genera exhibiting a dorsiventral inflorescence only. The moraceous genera which Bernbeck studied were *Dorstenia* and *Ficus*: in the former the dichasial arrangement of the earliest primordia on the flattened receptacle was clearly distinguishable, although later this became obscured by the simultaneous origin of many primordia, but in the latter, though the first bracts were arranged cymosely, the flower primordia all appeared almost simultaneously.

It has been observed in the present study that the inflorescence of *Artocarpus incisus* shows a similar degree of reduction, the flower primordia in both male and female heads arising almost simultaneously and in no discernible order. The same phenomenon had earlier been noted for *A. heterophyllus* (as *A. integrifolia*) by Subba Rao (1940) in a paper on the cytology and embryology of this species. In both these species interfloral bracts are lacking, but in others where they are present (e.g., *A. hispidus* and *A. gomezianus* ssp. *zeylanicus*) they arise and mature a little earlier than the flower primordia, though they bear no definite relation to the latter. In the less reduced inflorescence of *Treculia africana*, however, the sympodial arrangement of the first few interfloral bracts is evident. These bracts, like those of most species of *Artocarpus*, terminate in a peltate scale and at the apex of the inflorescence there is always one conspicuously large scale, with a few somewhat smaller ones arranged meridionally and the rest of the surface covered by scales of irregularly decreasing size.

The inflorescences of *Prainea* and *Artocarpus*, on the one hand, and of *Parartocarpus* and *Hullettia*, on the other, have, as has already been indicated, a fundamentally different structure and hence they will be considered independently in the following account. The structure of the inflorescences is illustrated in figs. 1-4,⁴ the species having been chosen both because they were typical and because, in *Artocarpus hispidus* and *Parartocarpus forbesii*, inflorescences preserved in alcohol were available.

In both male and female inflorescences of *Prainea* the perianths are tubular and free from each other, and are mixed with peltate to spatulate, long-stalked interfloral bracts. The male perianth is perforate or bilobed above and the apex of the female perianth is thick-walled and clavate, with a contracted mouth which is either perforate or very shortly 2-4-lobed. The female inflorescence of *P. papuana* is illustrated in fig. 1, a-e and the male inflorescence in fig. 3, a-c. As the female inflorescence ripens only

⁴ For convenience of reference the figures will be numbered consecutively throughout this series of papers.

those perianths in which seeds are formed enlarge markedly. These become fleshy and appear as conical to globose projections from the general surface of the inflorescence, which is formed by the apices of the unexpanded flowers and the heads of the bracts, giving the typical appearance shown in *fig. 1, c*. Beccari (1902), in recognizing the affinities of *Prainea* with *Artocarpus*, stated that the only difference between the genera lay in the structure of the female inflorescence, but this is only correct with respect to the reproductive organs.

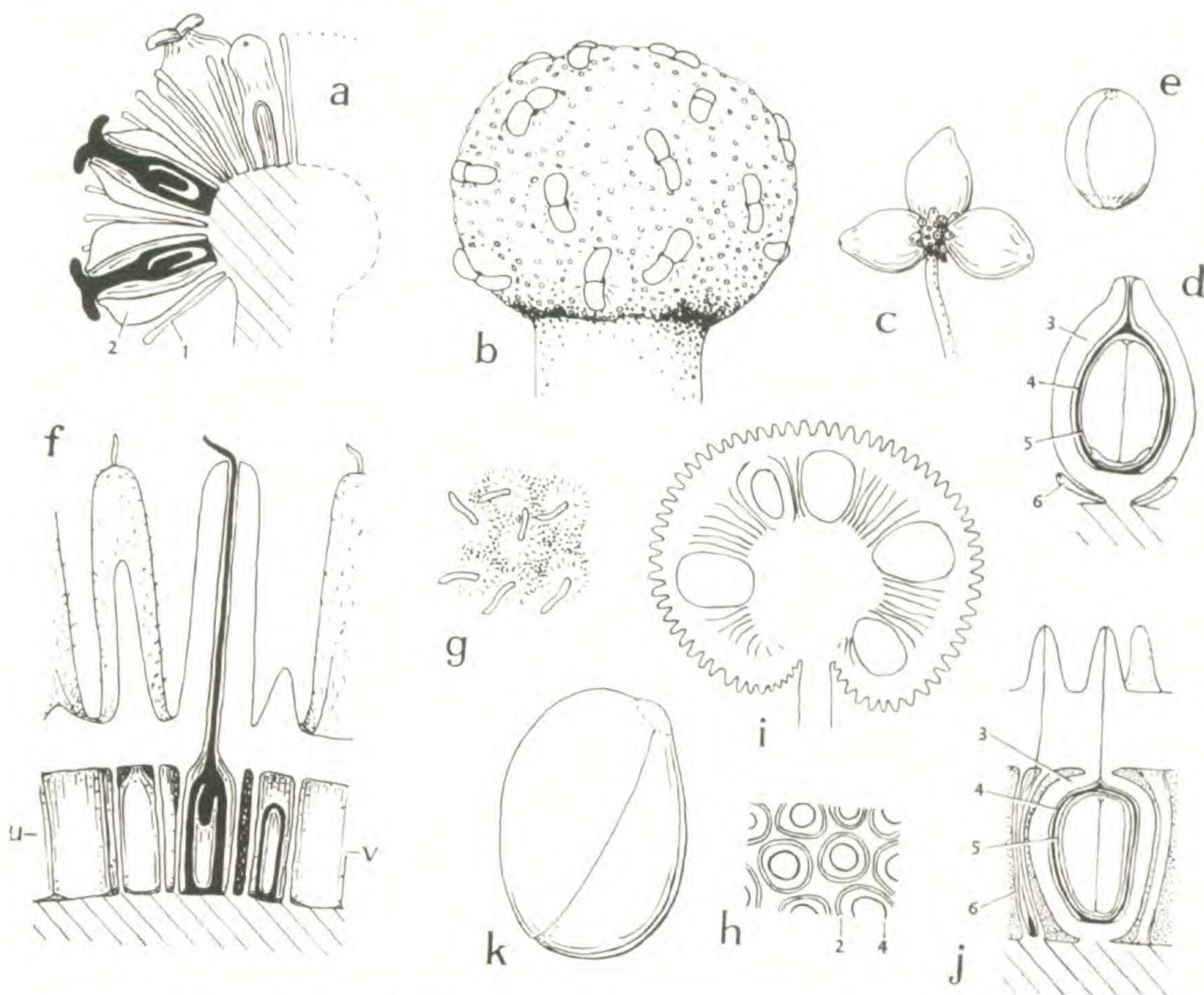


FIG. 1. The female inflorescence in *Prainea* and *Artocarpus*. a-e, *Prainea papuana*: a, b, longitudinal section and entire head at anthesis ($\times 5$); c, mature head ($\times \frac{1}{2}$); d, fruiting perianth in longitudinal section ($\times 1$); e, embryo ($\times 1$). f-j, *Artocarpus hispidus*: f-h, longitudinal section, surface view and tangential section in plane u-v at anthesis ($\times 10$); i, longitudinal section at maturity ($\times \frac{1}{2}$); j, part of the same ($\times 1$). k, *A. incisus*, embryo ($\times 1$).

Conventions used in *figs. 1-3*: ovaries and stamens are shown in black and receptacular tissue is crosshatched when cut in section. Abbreviations: 1, interfloral bract; 2, perianth; 3, fruiting perianth; 4, ovary; 5, testa; 6, unexpanded perianth; 7, involucre bract.

In the inflorescences of *Artocarpus* the flowers are also usually mixed with interfloral bracts, but these are frequently shed from the syncarp at or before anthesis and in some species they are altogether lacking. The perianths in the male inflorescence are likewise free from each other, varying from tubular to 2-4-partite, but in the female inflorescence the peri-

anths, which are tubular with a contracted and perforate apex, are fused with each other to form the characteristic syncarp from an early stage in development. This fusion is, however, only partial in most species and is of an unusual nature. Each perianth consists of a proximal region which is thin-walled and encloses the ovary, and a distal region with thickened walls and a narrow lumen through which the style passes to the exterior. Proximally the perianths remain free from each other, but distally they are connate, forming a continuous layer evidently capable of withstanding a considerable degree of tension as the syncarp matures. The perianths may

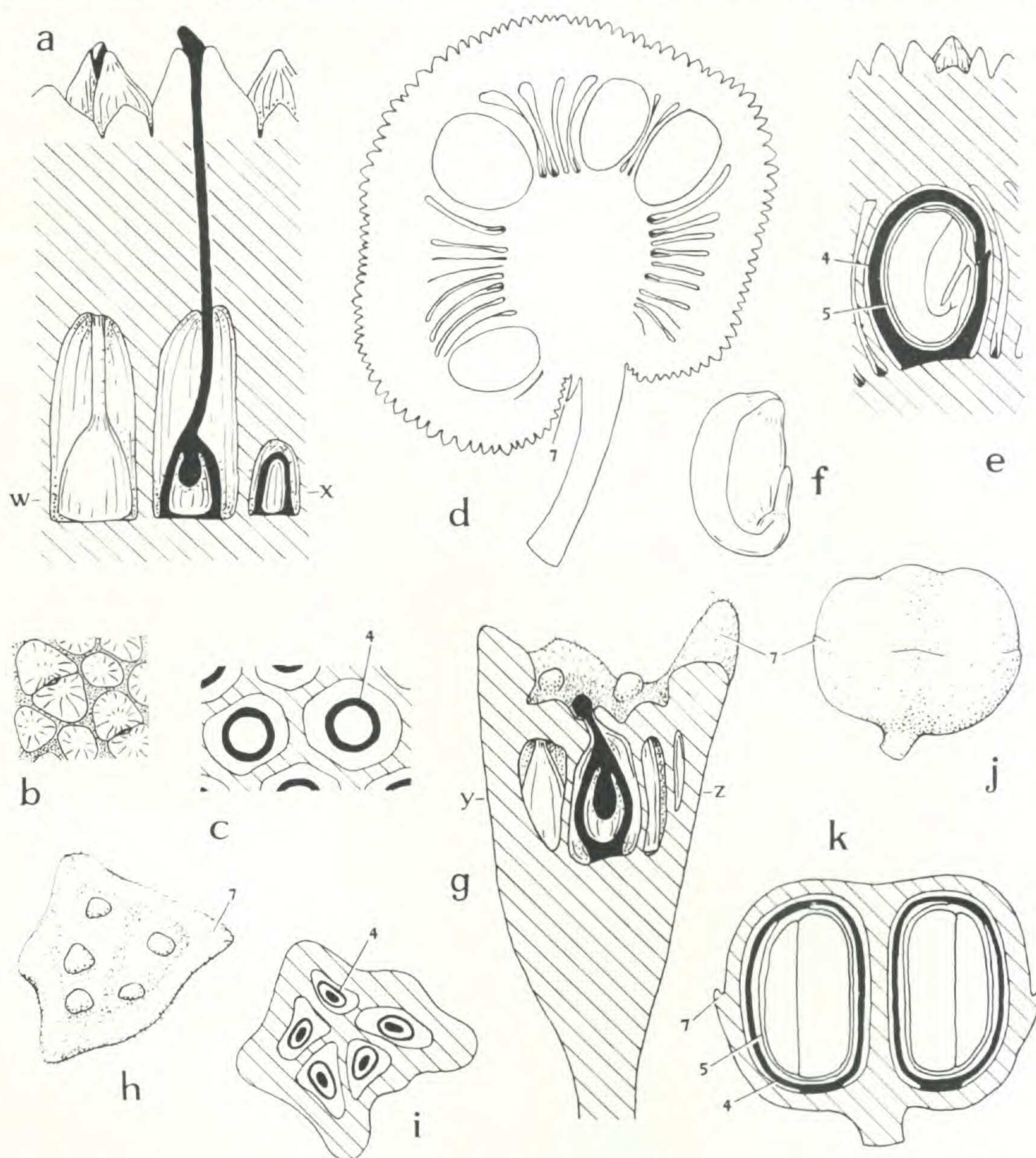


FIG. 2. The female inflorescence in *Parartocarpus* and *Hullettia*. a-f, *Parartocarpus forbesii*: a-c, longitudinal section, surface view and tangential section in plane w-x at anthesis ($\times 5$); d, longitudinal section at maturity ($\times \frac{1}{2}$); e, part of the same ($\times 1$); f, embryo ($\times 1$). g-k, *Hullettia dumosa*: g-i, longitudinal section, surface view and tangential section in plane y-z at anthesis ($\times 5$); j, mature head ($\times \frac{1}{2}$); k, the same in longitudinal section ($\times 1$, approx.).

be completely fused distally to form a smooth covering layer to the syncarp with perforations through which the styles are exerted at anthesis, or their apices may remain free and project as cylindric, conical or obtuse processes on the surface. In *Artocarpus* (subg. *Artocarpus*) *hispidus*, which is illustrated in fig. 1, *f-j*, the distal parts of the perianths are not completely fused to each other and the syncarp is echinate from their rigid, free apices. The longitudinal section of the female inflorescence at anthesis in fig. 1, *f* shows one perianth cut sagittally, while those on either side are cut in a tangential plane, and in those on the extreme right and left the proximal region and the free apices are seen in face view, the plane of the section having passed between neighbouring perianths. In contrast to *Prainea* the entire syncarp usually enlarges more or less uniformly although relatively few of the flowers set seed. In the proximal layer, however, where the perianths are free, only those containing seeds enlarge, and the others appear as narrow ribbons in the mature syncarp, as shown in fig. 1, *j*. In this and several other species of subgenus *Artocarpus*, including the Jack (*A. heterophyllus*), the proximal region of the fruiting perianths becomes fleshy and provides the edible portion of the syncarp, in addition to the seeds, which are often roasted, though in the seedless form of the Breadfruit (*A. incisus*) the entire head is eaten.

The syncarp has been examined in nearly all the species of *Artocarpus* subg. *Artocarpus* recognized in this study and the perianths have been found to be consistently free from each other at the level of the ovaries. The same structure is found in many species of subg. *Pseudojaca*, but in others the fusion between perianths is complete, although each perianth may still be distinguishable on the surface as an areole or papilla. In this subgenus the entire syncarp is fleshy and is eaten in a number of species.

It has been possible to examine very young inflorescences of *Artocarpus rigidus*, a species closely allied to *A. hispidus*, and the longitudinal section illustrated in fig. 4, *a* shows that the perianths are at first entirely free from each other. The later fusion must be due to the pressure exerted on each other by the thick-walled distal portions of the very closely set primordia. The thinner-walled proximal portions, having less resistance to pressure, would remain free.

The partial fusion of the perianths was described and illustrated for *Artocarpus heterophyllus* (under the name *Sitodium cauliflorum*) by Gaertner in 1788 and again in 1939 by Corner, writing on this species and on *Artocarpus integer*, but other authors have assumed that the ovaries were embedded in a solid mass of tissue. Nearly all have regarded this tissue as representing the perianths, but Baillon, stated (1863) that the tissue surrounding the ovaries must be axial in origin, on the grounds that the belated fusion of neighbouring parts is very rare, as is indeed the case. He was able to study material of *Artocarpus incisus* preserved in alcohol, but, nevertheless, observing the very young pistils each in the centre of a ring-like emergence, he described them as becoming gradually more deeply sunken in pits of the receptacle and failed to notice the more complex adult structure.

In *Prainea* the male and female inflorescences are more or less globose and are not always easily distinguishable before anthesis, but in *Artocarpus* there is a considerable range of variation especially in the male head, and the two sexes usually differ markedly in size and shape. In neither genus is there a clearly differentiated involucre, although there may be few sessile bracts similar to the interfloral bracts at the base of the head. In *Artocarpus* there may be a slight enlargement of the top of the peduncle and in *A. heterophyllus* this forms a distinct annulus.

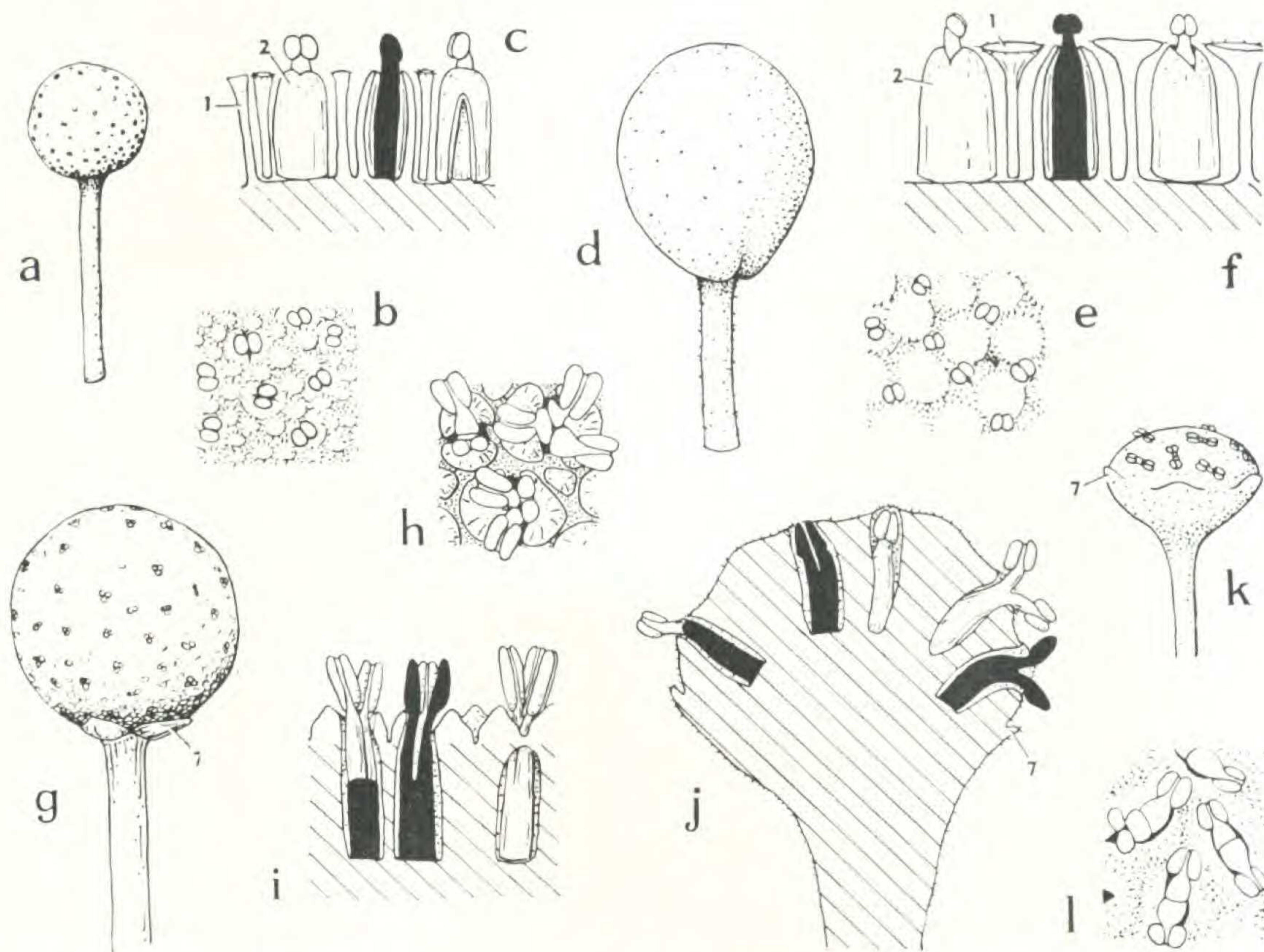


FIG. 3. The male inflorescence. a-c, *Prainea papuana*: a, entire head ($\times 1$); b, c, surface view and longitudinal section ($\times 5$). d-f, *Artocarpus hispidus*: d, entire head ($\times 1$); e, f, surface view and longitudinal section ($\times 20$). g-i, *Parartocarpus forbesii*: g, entire head ($\times 1$); h, i, surface view and longitudinal section ($\times 5$). j-l, *Hullettia griffithiana*: k, entire head ($\times 2$); l, j, surface view and longitudinal section ($\times 5$).

In *Parartocarpus* the inflorescences of the two sexes are similar to each other in structure, with both stamens and ovaries contained in cavities in the apparently continuous tissue of the capitula. Careful examination has revealed no sign of fusion having taken place between neighbouring perianths in the walls separating the cavities and developmental studies show that they are intercalary in origin. Details of the structure in *Parartocarpus forbesii* are shown for the female inflorescence in fig. 2, a-f and for the male inflorescence in fig. 3, g-i; comparison of the tangential section of the female inflorescence at the level of the ovaries (fig. 2, c) with that of *Artocarpus hispidus* (fig. 1, h) will show the difference between the

syncarps of the genera. The surface of the receptacle in *Parartocarpus* is closely covered by indurated processes, which are acutely conical or spinous in *P. forbesii*. Some are arranged in groups of two to four around the openings of the cavities containing the stamens or ovaries, and are fused basally to each other around the opening. The rest, which are identical in appearance, are free from each other and cover the intervening surface, bearing no relation to a cavity. The processes surrounding the openings are fused to each other only at the base at anthesis, but, since they grow from below, the fusion becomes more marked during the ripening of the syncarp. In spite of its different origin, this syncarp is superficially very similar to that of some species of *Artocarpus* in which the perianth apices are indurated.

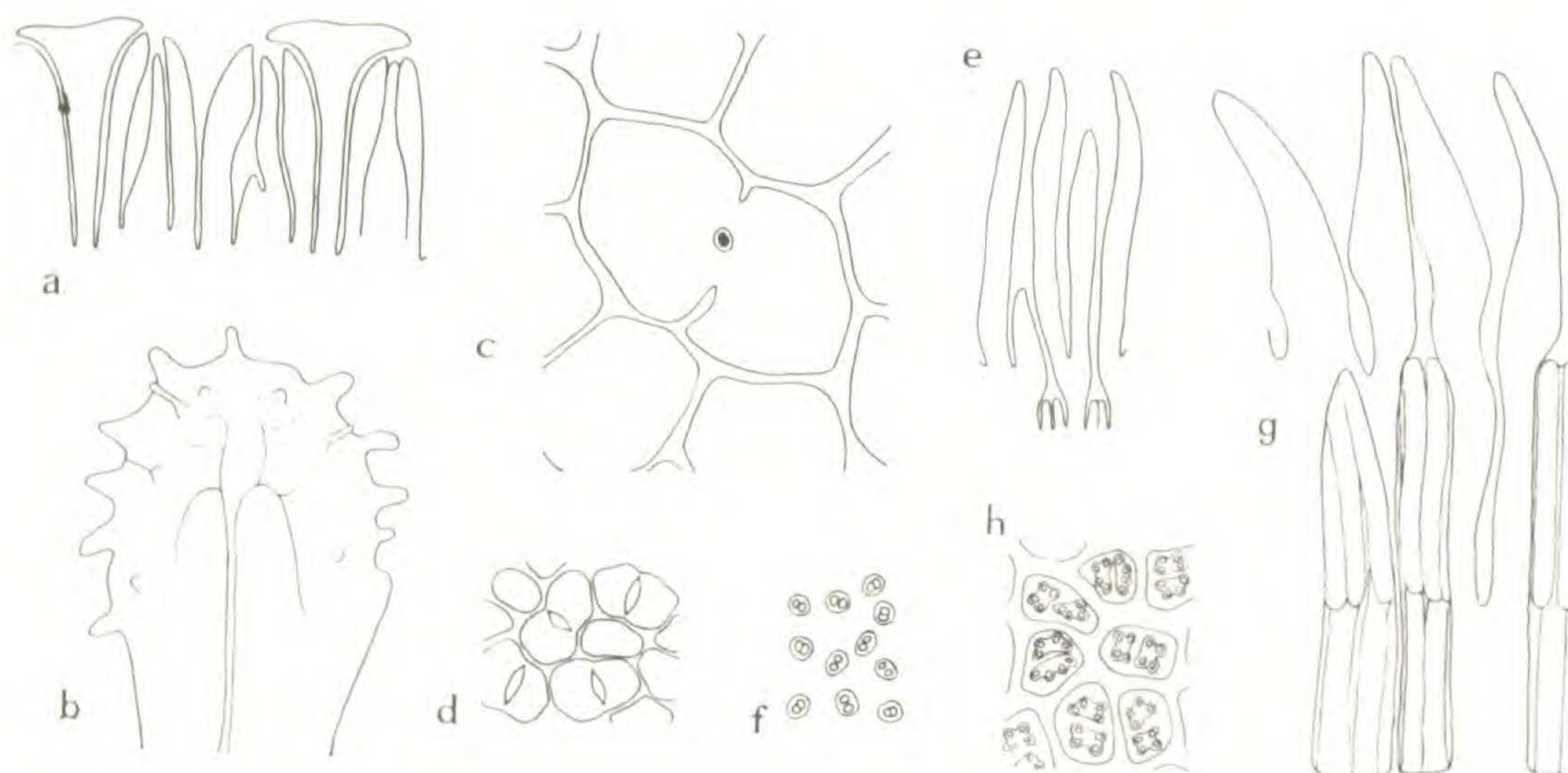


FIG. 4. Details of inflorescence structure. a, b, Longitudinal sections of young female inflorescences in *A. rigidus* ($\times 12.5$) and *A. styracifolius* ($\times 2.5$). c, d, Transverse sections through bases of perianths in female inflorescence of *Parartocarpus venenosus* at anthesis and in male inflorescence of *P. forbesii* before anthesis ($\times 5$). e-h, Development of male head in *Parartocarpus bracteatus*: e, f, longitudinal and tangential sections from head 7 mm. in diameter ($\times 10$); g, h, the same from head 25 mm. in diameter ($\times 5$).

The development of the inflorescences is illustrated by the sections, both longitudinal and tangential at the level of the stamens, through male heads of *Parartocarpus bracteatus* in fig. 4, e-h. In this species the processes are spinous and the considerable enlargement of the cavities relative to the processes during their growth is evident on comparison of the figures. In the younger inflorescence (diameter of the head 7 mm.) the stamens are merely finger-like projections, while in the older one (diameter 25 mm.) they are nearly at anthesis. It has not been possible to examine any younger stage but it is probably justifiable to assume that the stamens arise between the processes on the surface of the receptacle and are only later enclosed within cavities. The intercalary origin of the walls is confirmed by the vertical lines of cells that are seen in longitudinal section. The processes are indurated from an early stage in development and can

therefore grow only at the base, while they must also enlarge laterally to cover the increasing surface area of the receptacle. It has not been possible to determine whether the processes surrounding each cavity are originally free, or whether they arise from a ring of tissue surrounding the androecium or gynoecium.

Varying opinions have been expressed as to the identity of the processes. In view of the similarity of the "fertile" and "sterile" processes it may be assumed that they are all equivalent; thus they presumably represent either perianths or interfloral bracts. Baillon, who was working with limited material of the male inflorescence, inaccurately stated in the original description of *Parartocarpus beccarianus* (1875) (= *P. venenosus* (Zoll. & Mor.) Becc.) that the stamens were intermingled with stalked bracts (the processes on the surface representing their heads), and hence supposed that the difference between this and the male inflorescence of *Artocarpus* lay in the absence of perianths. Boerlage (1897), who described the same species independently under the name *Gymnartocarpus venenosa* (based on *Artocarpus venenosa* Zollinger & Moritzi) likewise distinguished it from *Artocarpus* by the absence of perianths, but he described the stamens and ovaries correctly as sunken in cavities of the receptacle, regarding the processes alone as representing bracteoles. He failed to observe the fusion of the processes grouped around each cavity, which is not conspicuous in this species, since they are short and often truncate. The fusion is shown in the tangential section through the bases of the processes in *fig. 4, c*. Beccari, in discussing the inflorescence structure of *Artocarpus* and *Parartocarpus* in 1902, was the first to note the fusion of some of the processes in the latter. He considered that they represented the apical lobes of tubular perianths, which were completely fused to each other below, and that the free processes represented the solid apices of sterile perianths. While he realised that the processes thus differed from the tubular perforate perianth apices of *Artocarpus* he did not observe any difference in the internal structure.

Although the fusion of the processes around each cavity indicates that Beccari's interpretation is correct, apart from the fact that the tissue enclosing the stamens and ovaries is intercalary in origin and only the processes themselves can be regarded as representing the perianths (and even in these the base is also intercalary), the allied African genus *Treculia* must here be considered, since its less reduced condition may throw light on the structure of *Parartocarpus*.

In *Treculia africana*, well differentiated perianths, interfloral bracts and basal involucre are all present (illustrated in Engler, 1898, *t.* 12-14). The stalks of the abundant interfloral bracts are fused for about half their length, so that the flowers are enclosed in cavities between them. That this tissue represents the stalks of the bracts is shown by its continuity with the free distal portions of the stalks and the abrupt transition to receptacular tissue below the level of the flowers. In the male inflorescences the flowers consist of (2-)3-4(-5) stamens enclosed in a membranous tubular perianth. In the female inflorescence each ovary may be

accompanied by up to four linear perianth segments, and numerous abortive male flowers are also present. In this species each bract is terminated by a peltate scale, but in other species of the same genus the shape of the heads of the bracts is various. In *Treculia zenkeri* Engler (l.c., t. 15) the bracts have some peltate and some capitate heads, while in the male head of *Treculia obovoidea* N.E.Br. (as examined in *Zenker 2526*) the bracts terminate in minute spinous processes surrounding the cavities containing the flowers and bluntly conical processes covering the intervening surface. Hutchinson (1917) considered that *Acanthotreculia winkleri* Engler (1908) probably represented the female inflorescence of the latter species and in this the free spinous processes surrounding each emerging style were described as conspicuous and strongly differentiated from the other short and obtuse processes. The processes in both *Treculia zenkeri* and *T. obovoidea* have a general similarity to those on the surface of the inflorescences of *Parartocarpus* and the possibility must be considered that in the latter the bracts have secondarily assumed the function of perianth segments, those surrounding the openings of the receptacular cavities becoming partially fused to give added protection; that perianths containing the stamens and ovaries have been lost; and that walls of intercalary origin enclosing the latter have replaced the stalks of the now sessile bracts.

The inflorescence structure of *Hullettia* is fundamentally similar to that of *Parartocarpus*, although interfloral bracts and perianths are apparently entirely lacking and the fleshy, pubescent receptacle is naked, having perforations in the surface leading to cavities containing either stamens or ovaries. The female inflorescence of *Hullettia dumosa* is illustrated in fig. 2, g-k and the male inflorescence of *H. griffithiana* in fig. 3, j-l. No material has been available for studies in development, and the homology of the structure with that of *Parartocarpus* is inferred from examination of the inflorescences at anthesis and maturity and from other characters which the genera have in common.

The most immediately obvious of these similarities is that in *Hullettia*, as in *Parartocarpus* and *Treculia*, there is a clearly differentiated involucre. In *Parartocarpus* this consists of three to eight basal bracts which are triangular to ovate and indurated or thickly coriaceous. In *Hullettia* there are three to six fleshy flattened triangular projections which at anthesis are marginal on the obturbinate or pulvinate receptacle and on the subglobose mature syncarp vary from a basal to an equatorial position. In both genera the bracts may be somewhat obscured, especially on the mature syncarp of *Hullettia*. In *Parartocarpus* the inflorescences are globose or nearly so, like those of *Prainea*, and the male and female inflorescences can only be identified before anthesis by dissection, but in *Hullettia* it is only the very young inflorescences that are indistinguishable externally.

Details of the flowers have not been included in this discussion of the generic characters of the inflorescences, but those of the ovary will be considered in the following section. In *Prainea* and *Artocarpus* there is little variation in the male flowers and in distinguishing the species the entire inflorescence is the unit of variation. However, the male perianth

in *Artocarpus* subg. *Artocarpus* is nearly always tubular and bilobed above, whereas in subg. *Pseudojaca* it is frequently 2–4-partite, and, in the former, slight differences in the size of the anthers are of some assistance in establishing the subdivisions. There are also small differences in the stamens of the various species of *Parartocarpus* and *Hullettia*.

In conclusion, some aspects of the variability of the inflorescence within *Artocarpus*, which is in marked contrast to its relative uniformity within the other genera, will be commented on. In the syncarp, as in the male inflorescence, there is some overlapping in the characters of the two subgenera, so that they are most readily defined by the characters of the shoot. However, in subgenus *Pseudojaca* the syncarp is always more or less globose, with a surface varying from smooth to tuberculate, but never (except in *A. styracifolius*, discussed below) bearing distinctly elongate processes. In subgenus *Artocarpus*, on the other hand, the syncarp is always covered (at least at anthesis) by distinct processes, except in *A. sepi-canus* and *A. kemando*, and in these, as in a majority of the other species, the syncarp is ellipsoid to cylindric.

The variety in the shape of the processes on the syncarp in *Artocarpus* subg. *Artocarpus* is considerable and will be illustrated in a plate accompanying the key to the subgenus. In a few species solid sterile perianths are present with elongate apices projecting markedly beyond those of the fertile perianths; in *A. multifidus*, *A. elasticus*, *A. sericicarpus* and *A. tamaran* the dimorphism is complete, but in *A. teysmannii* intermediates occur, all except the longest apices being perforate. This feature has either been unnoticed or its significance has been unrecognized by earlier authors. Elongate sterile perianths also occur in the male inflorescences of the first and last of these species. That these elongate processes represent sterile perianths and not enlarged interfloral bracts is shown by the finding of the latter in the same inflorescences, and by the close similarity of the perforate and solid processes in the syncarp.

In subgenus *Pseudojaca*, on the other hand, the flexuous, solid, terete processes that cover the surface of the syncarp of *A. styracifolius*, and between which the styles emerge through perforations in the surface, appear to be enlarged interfloral bracts. They have a single longitudinal vascular bundle, and in the young syncarp they look very similar to the clavate interfloral bracts found in the male inflorescence. A longitudinal section at this stage is shown in *Fig. 4, b*.

STRUCTURE OF THE SEED AND ITS GERMINATION

These genera are characterized by large seeds which have little or no endosperm and no period of dormancy or ability to withstand desiccation. Differences in the shape and orientation of the embryo and in the mode of germination confirm alliances indicated by the structure of the inflorescences. The ovule is pendulous at anthesis, being attached at or a little below the apex of the ovary, and the style is terminal or nearly so, but in the mature ovary the position of the style and the attachment of the seed

vary from apical to sub-basal, owing to differential growth in the walls of the ovary.

In *Prainea papuana*, the only species of the genus of which material was available for detailed study, the style is strictly terminal throughout, but, while at anthesis the ovule is attached laterally slightly below the apex of the ovary, at maturity it is sub-basal. The mature ovary is membranous and the testa is totally absorbed except for a thickened basal saucer-shaped region, at one side of which is the hilum. The embryo, which is illustrated in *fig. 1, e*, is symmetrical, with two equal cotyledons having their long axes parallel to the median plane of the ovary but their appressed faces at an angle of about 45° to it. The radicle and plumule are small and apical.

In *Artocarpus* there is great variation in the ovary and embryo and also in the consistency and relative thickness of the fruiting perianth, ovary and testa. In subgenus *Artocarpus* the terminal or lateral position of the style in the mature ovary delimits two natural groups of species. The seed is attached just below the base of the style and, since the radicle is usually directed approximately at the hilum, in the first group the embryo is longitudinally aligned and the radicle is apical, whereas in the second the long axis of the embryo is more or less oblique and the radicle is ventral. In the first group the appressed faces of the cotyledons are at an angle of $30-90^\circ$ to the median plane of the ovary and the radicle and plumule are apical and minute so that the appearance of the embryo and its orientation relative to the ovary are similar to *Prainea*, although the hilum is apical instead of sub-basal. In these species the inner wall of the ovary forms a horny endocarp, while the exocarp decays leaving the "seed" free within the proximal region of the perianth which may be thickened and fleshy. In species in which the style is lateral or sub-basal in the mature ovary and the long axis of the embryo is hence more or less oblique, the appressed faces of the cotyledons may be in the median plane of the ovary (in which case the embryo is usually symmetrical), or they may also be oblique or at right angles to the median plane (in which case one cotyledon lies above the other in the seed and is frequently reduced in size). Such an embryo is illustrated in *fig. 1, k*. The variation in this second group will be discussed in more detail in considering the subdivision of subgenus *Artocarpus*. In this group the cotyledonary petioles and the radicle lying between them are relatively well developed and, if the latter is large enough, it is curved downward. The chalaza is always basal, with a conspicuous ventral raphe, so that in the first group the embryo is anatropous, whereas in the second it is campylotropous.

In *Artocarpus* subg. *Pseudojaca* the style is terminal or nearly so and the embryo is longitudinally aligned, with the appressed faces of the equal cotyledons in the median plane of the ovary or at varying angles to it. In some species of this subgenus, also, the seed is enclosed by an indurated endocarp which lies free in the cavity of the perianth at maturity.

The primary difference between the embryo in these genera and in *Parartocarpus* is that in the latter it is folded. The ovary has a terminal

style at anthesis, but at maturity it is lateral and the hilum lies just above it. The ovary wall differentiates into a bony endocarp and an exocarp which finally decays. The testa is attached to an indurated hilar plug and is thin-walled, with a relatively small apical vascular cap. The embryo fills it almost completely but, unlike *Artocarpus*, there are distinct remains of the endosperm in the region of the hilum. The markedly unequal cotyledons are appressed to each other and are incumbent, being folded transversely a little above the base so that the large, straight radicle lies along the median line of the inner and smaller cotyledon. The plane of the appressed faces of the cotyledons is longitudinal and at right angles to the median plane of the ovary. The tips of the cotyledons are enclosed in the vascular cap of the testa, which makes a distinct indentation in them, and the radicle lies on the side of the seed facing the style, its tip being directed upward to the hilum and enclosed in a pocket of endosperm. The embryo of *P. forbesii* is shown in fig. 2, *f*. The same type of embryo occurs in *Treculia* (*africana*) and has been illustrated by Trécul (1847) and Engler (1898) (but in *Acanthotreculia* Engler (1908) the embryo is shown with very unequal, straight cotyledons and a small, apical radicle).

The embryo of *Hullettia*, on the other hand, is straight, with equal or slightly unequal cotyledons arranged longitudinally; the small radicle, however, is basal. The ovary is pergamaceous and the testa has a shallow, thickened, apical cap (not shown in fig. 2, *k*) attached centrally, immediately below the subterminal style, and making an indentation in the tips of the cotyledons, but is otherwise thinly membranous. Thus, whereas in *Prainea* and *Artocarpus* the chalazal region is basal, in *Parartocarpus* and *Hullettia* it is apical (relative to the ovary), and since the tips of the cotyledons are in contact with this region, except in some species of *Artocarpus*, the orientation of the embryo with respect to the ovary is also reversed.

It has been possible to study germination in the following species of *Artocarpus*: (subg. *Artocarpus*) *A. rigidus*, *A. integer*, and *A. heterophyllus*, and (subg. *Pseudojaca*) *A. borneensis*. In addition I have been able to use Mr. Corner's notes on germination in *Artocarpus* (subg. *Artocarpus*) *anisophyllus*, *A. lanceifolius* and *A. elasticus* and *Parartocarpus bracteatus* and *P. forbesii*, and to examine herbarium specimens of seedlings of *Artocarpus incisus* and *A. nobilis*.

Germination in *Artocarpus* and *Parartocarpus* differs chiefly in whether or not there is elongation of the hypocotyl. In *Artocarpus* there is no elongation, and germination is hence hypogeal. The cotyledons usually remain enclosed within the testa and the plumule is enabled to emerge from between them by the elongation of their petioles (illustrated for *A. hirsutus* and *A. chaplasha* in Troup, 1921, figs. 323, 325). In *A. heterophyllus* (l.c., fig. 324, and Gaertner, 1788) and *A. integer*, however, the cotyledons separate to allow the emergence of the plumule. A further variation occurs in subgenus *Artocarpus* in the nature and arrangement of the first leaves borne by the seedling. The first pair subsequent to the seed leaves may be opposite and fully developed and be followed by spirally

arranged leaves (*A. anisophyllus*, *A. lanceifolius*, *A. rigidus*, *A. chaplasha*, *A. hirsutus* and *A. nobilis*) or the leaves may be spirally arranged from the first, the youngest being scale leaves (*A. incisus*, *A. heterophyllus*, *A. integer* and *A. elasticus*). The two types correspond, but only approximately, to the species groups distinguished above by the terminal and lateral position, respectively, of the style, and will likewise be discussed in more detail under subgenus *Artocarpus*. In *Artocarpus* subg. *Pseudojaca* the seedling bears scale leaves before the fully developed leaves, as in the second group above, but in *Artocarpus borneensis* (ssp. *griffithii*) these are strictly alternate and distichous from the first. It is not clear from Troup's illustration (l.c., fig. 326) of *A. lakoocha* whether the leaves are spirally or distichously arranged. Photographs of seedlings of *A. rigidus* and *A. borneensis* are reproduced in fig. 5.

In *Parartocarpus* germination is epigeal and the hypocotyl elongates markedly, carrying the folded cotyledons well above the ground. As they straighten and open out, becoming green and photosynthetic, the endocarp and testa are split off. The plumule grows out from between them and the first pair of leaves is opposite, with paired stipules, but the later leaves are spirally arranged, each with a single stipule. The seedlings of *Treculia africana* show an exactly similar mode of germination.

MORPHOLOGY OF THE SHOOT

The morphological characters of the shoot which are of importance in distinguishing the genera under review are principally those provided by the arrangement of the leaves and by the stipules, which enclose the terminal bud and are either intrapetiolar or lateral to the base of the petiole, being paired except in *Parartocarpus*. They are illustrated in fig. 6. It is in these characters that the most easily discernible distinctions are to be found between the two subgenera of *Artocarpus*. In subg. *Artocarpus* the leaves are spirally arranged and the stipules are intrapetiolar and amplexicaul, leaving annulate scars, whereas in subg. *Pseudojaca* the leaves are strictly alternate and distichous and the stipules are non-amplexicaul, leaving lateral or partially intrapetiolar scars. The latter arrangement is also found in *Prainea* but the leaves of this genus can usually be recognized by the abruptly and narrowly acuminate apex and the conspicuous and regular inarching of the lateral veins (in addition to details of the anatomy). In *Parartocarpus* the leaves are spirally arranged and in the axil of each is a single non-amplexicaul stipule which forms a scar extending slightly to either side of the petiolar scar. J. J. Smith (1922) was the first author to realize that these stipules were single and not paired. In the seedling, as already mentioned, they may be paired or have a bifid apex, indicating that each has originated from two stipules fused along their intrapetiolar margins. The leaf arrangement, together with the non-amplexicaul stipular scars, distinguishes the genus from both the preceding ones. The leaves of *Hullettia* are also spirally arranged but the stipules



FIG. 5. Seedlings of *Artocarpus*; left, *Artocarpus* (subg. *Artocarpus*) *rigidus*; right, *Artocarpus* (subg. *Pseudojaca*) *borneensis*; insets, details of stipules.

are distinctive, being linear, acute and frequently persistent. They are lateral to the leaf-axils and the scars are small and round.

Differences in the arrangement of the foliage are associated with the two types of phyllotaxy. In the groups with spirally arranged leaves the ultimate shoots and usually also the main branches are ascending. In *Parartocarpus* and *Hullettia* the leaves are markedly clustered at the tips of the shoots and there is greater elongation of the internodes at the base of each lateral branch, so that one leaf cluster is separated from the next.

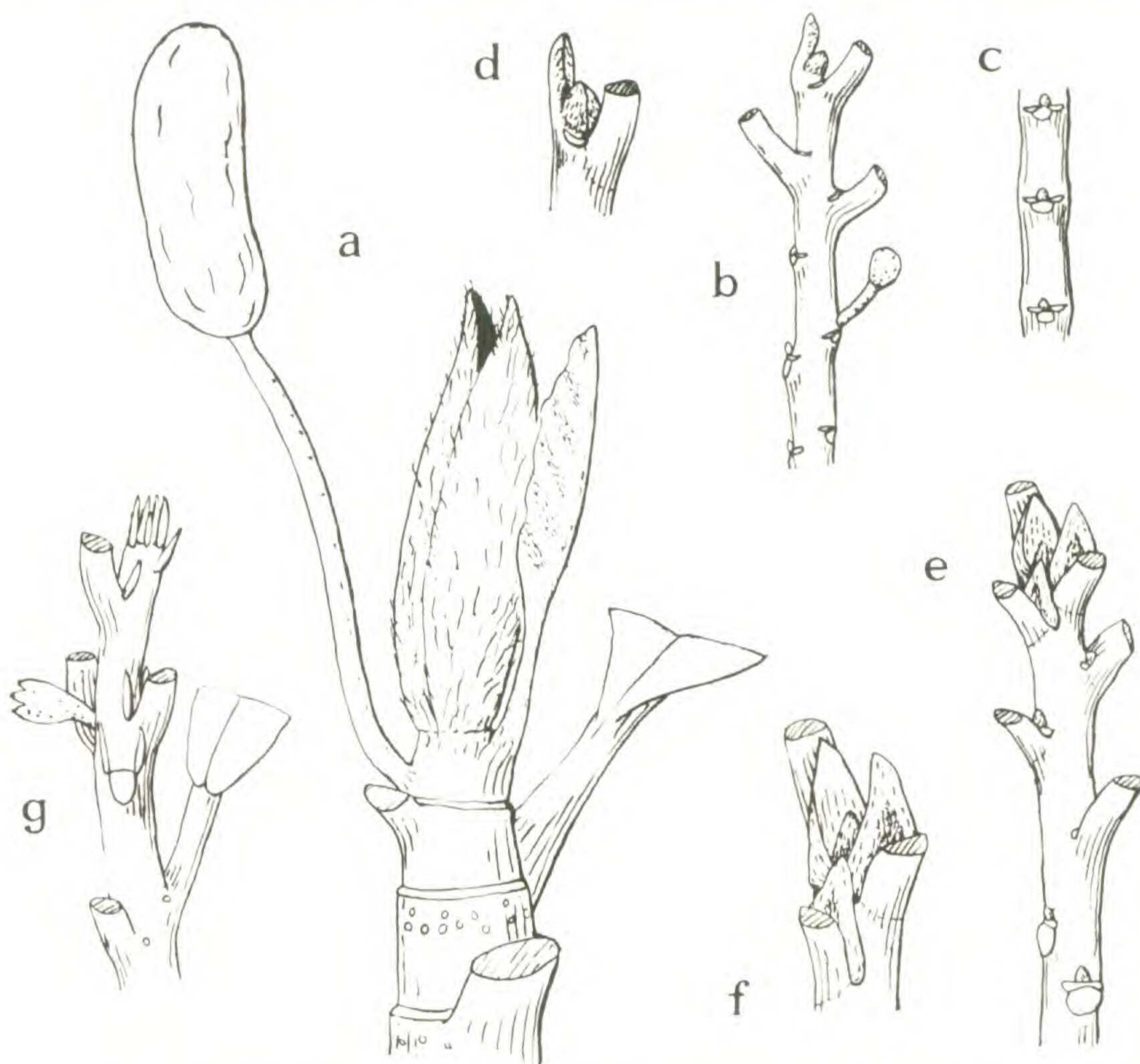


FIG. 6. Details of stipules; a, *Artocarpus sericicarpus* ($\times 1$); b, c, *A. gomezianus* ssp. *zeylanicus* ($\times 1$); d, terminal bud of the same ($\times 2$); e, *Parartocarpus bracteatus* ($\times 1$), f, terminal bud of the same ($\times 2$); g, *Hullettia dumosa* ($\times 1$).

In the groups with alternate leaves, on the other hand, at least the ultimate shoots are more or less applanate. As already mentioned, study of the seedlings of species belonging to both subgenera of *Artocarpus* has shown that the difference in leaf arrangement may exist from the earliest stage.

Leaf form in *Artocarpus* is variable, ranging from simple to pinnatifid. In most species the adult leaf is simple, but in one group within subg.

Artocarpus it is frequently pinnatifid, while in another species, *A. anisophyllus*, it is pinnate. In many other species of this subgenus the juvenile leaves are more or less pinnatifid and sometimes very large — to six feet in length in *A. elasticus* (Corner, 1940). *Artocarpus tamaran* is remarkable in having a nearly pinnate juvenile leaf, distinguished from that of *A. anisophyllus* by a continuous wing of lamina along the rachis. In some species of subg. *Pseudojaca* the juvenile leaves are irregularly pinnatifid or the lamina may be reduced to a sinuous wing along the midrib, but in the rest, as in the other genera, the leaf is always entire and the juvenile leaf is merely elongate. Juvenile leaf-forms are shown in fig. 7. As noted by Corner (1940) the pinnate leaves of *Artocarpus anisophyllus* are unusual in falling as a whole instead of disarticulating at the base of each pinna.

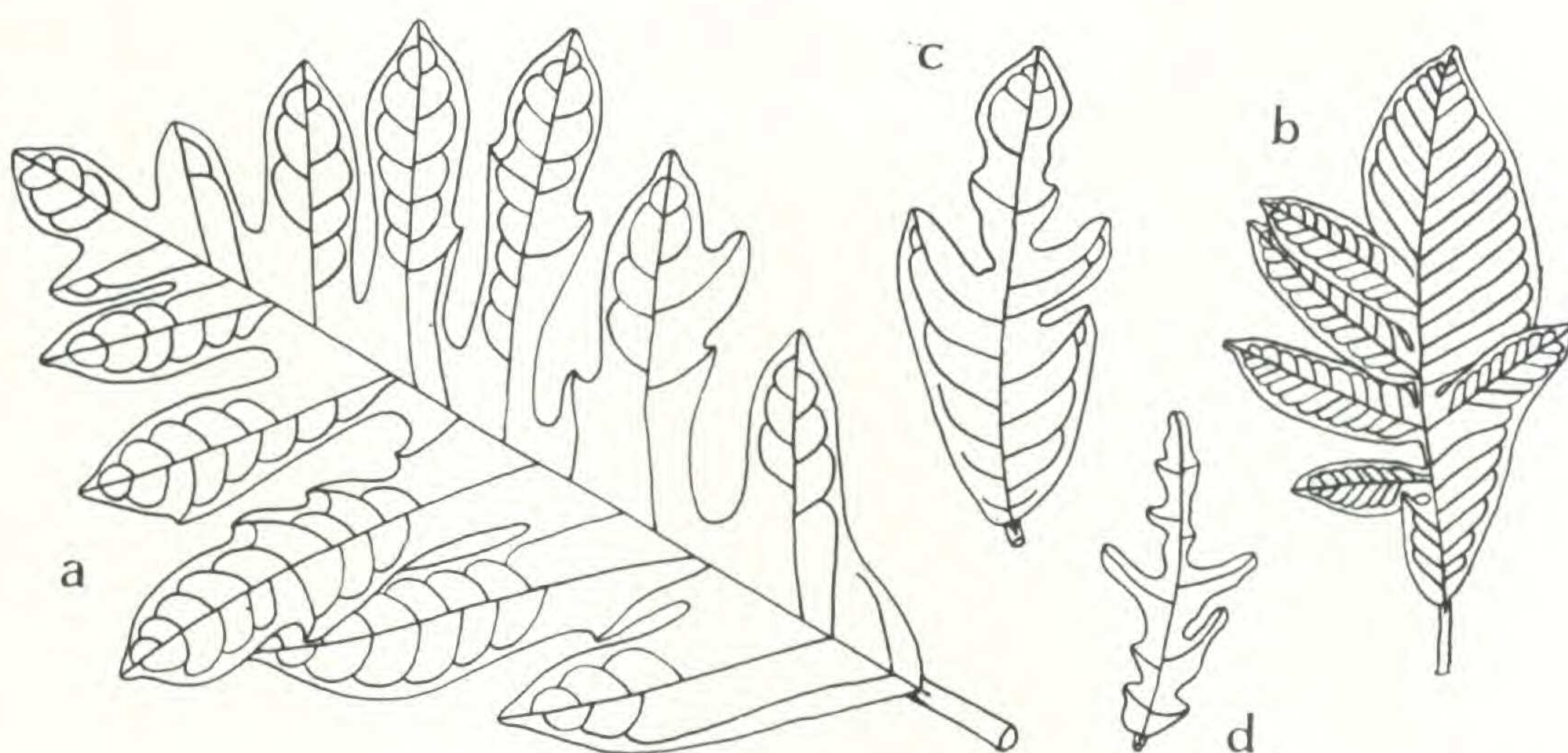


FIG. 7. Juvenile leaves in *Artocarpus*; a, *A. odoratissimus*; b, *A. tamaran*; c, d, *A. dadah* ($\times 1/7$).

In the field *Artocarpus* and *Parartocarpus* are easily distinguished by characters of the bark. In *Artocarpus* the bark on the roots is red and that on the trunk peels off in flakes. In *Parartocarpus* the bark of the roots is yellow, while the trunk is covered by numerous large and prominent lenticels (conspicuous in the photograph in Browne, 1955).

LEAF ANATOMY

A detailed account of the leaf anatomy of the Artocarpoideae and Conocephaloideae was published by Renner in 1907. From this it may be concluded that the most important anatomical characters distinguishing the genera under consideration are those of the microscopic glandular epidermal hairs and of the spongy mesophyll. Renner considered that the fact that leaf anatomy of *Prainea* was in some ways intermediate to that of the two subgenera of *Artocarpus* necessitated the unification of the two genera, but this view is here rejected as a misinterpretation of the vegetative characters.

Renner's observations have been repeated in the course of this revision and expanded to cover all the species here recognized. They have in general been confirmed, but in the following discussion a few points of disagreement are indicated. The leaves were examined by means of surface and transverse sections cut from fragments of herbarium specimens boiled up in water, or from material preserved in alcohol when available. The sections were mounted in a solution of polyvinyl alcohol and lactic acid (Metcalf and Richardson, 1950).

In addition to normal epidermal hairs the Artocarpoideae have gland-hairs on or sunken into the surface of the leaf, with a unicellular stalk and a variously shaped head. Renner stated that he was unable to find any anatomical characters distinguishing the tribes of the Artocarpoideae, but this may have been due in part to the fact that some genera were misplaced or studied from misidentified specimens. However, the Old World genera of Artocarpeae do show a wide range of variation in the gland-hairs, especially within the genus *Artocarpus*.

In *Prainea* and *Artocarpus* subg. *Artocarpus* the heads of the gland-hairs are 4–16-celled with a thick-walled stalk. In the former they are always and in the latter they are frequently sunken in pits in the epidermis. In *Prainea* the heads are depressed-globose and divided by vertical and horizontal walls into four to eight cells. In *Artocarpus* subg. *Artocarpus* the heads are either globose or depressed-globose with one or two tiers (rarely four) of four to six cells, or they are flattened and peltate with eight or rarely sixteen cells. An account of the gland-hairs is included in each specific description for this subgenus. In several species there is a hypodermis of cells which are either isodiametric or elongate in surface view. Both the gland-hairs and the hypodermis provide characters of taxonomic value and will be discussed further in considering the classification of the species of the subgenus.

In most species of *Artocarpus* subg. *Pseudojaca*, on the other hand, the gland-hairs have a unicellular globose head and a thin-walled stalk. Renner found the head to be 2–4-celled in *Artocarpus lakoocha* and in this study it also has been found to be 1–6-celled in *A. tonkinensis*. The gland-hairs of *Parartocarpus* likewise have a thin-walled stalk and a unicellular head, but the latter is markedly elongate and thus cylindric. In *Hullettia*, which was omitted by Renner as being of doubtful affinities, the gland-hairs have a thick-walled stalk and a globose unicellular head. According to Renner the gland-hairs of *Treculia* have an elongate head often divided by a longitudinal wall. In none of these are the gland-hairs sunken, except for a few species of *Artocarpus* subg. *Pseudojaca* in which they are only slightly so, and in none is there a hypodermis.

In the characters of the spongy mesophyll the two subgenera of *Artocarpus* again differ widely, while *Prainea* occupies a somewhat intermediate position. All the genera being studied have a bifacial leaf with one or two rows of palisade cells, and a well developed spongy mesophyll. This is more or less compact in *Artocarpus* subg. *Pseudojaca*, *Parartocarpus* and *Hullettia*, but in *Artocarpus* subg. *Artocarpus* it is extremely loose, consisting

by divergence from a common ancestor with *Prainea*. The anatomical characters, in conjunction with the difference in leaf and stipular arrangement, provide the best evidence that the subgenera of *Artocarpus* represent natural groups.

In their indumentum (apart from the gland-hairs) all the genera are variable, except for *Prainea*, in which the leaves are glabrous. The hairs frequently have enlarged bases and papillate walls, though, as was noted by Renner, there may be a few hairs with hooked tips and these are always smooth walled. In *Prainea* there are likewise enlarged cells in the epidermis which may be produced into a very short point. In *Artocarpus* the hairs are usually restricted to the veins, but in some species of subg. *Pseudojaca* nearly all the cells of the areolae grow out to form thin-walled, often crisped hairs, so that the lower surface appears greyish-glaucous from the minute tomentum. In *Hullettia* there are numerous enlarged cells with strongly thickened and narrowly pitted walls in the lower epidermis, which bear hairs of varying length and cause the lower surface to appear minutely punctate under a lens.

GENERAL CONCLUSIONS

The conclusions reached in the foregoing discussion are summarized below in the order in which the characters were taken up.

The inflorescences of *Prainea* and *Artocarpus* are covered by well developed perianths enclosing the stamens and ovaries and mixed with interfloral bracts, but they lack a clearly differentiated involucre. In the female inflorescence of *Artocarpus* the perianths are fused to form a syncarpium. Dissection shows that the proximal portions of the perianths, enclosing the ovaries, usually remain free, while the distal portions fuse, either completely or leaving the apices free, to form an external wall. The perianths have been found to be completely free in the very young inflorescence. In some species (in subg. *Pseudojaca*) the fusion between the perianths is complete, but it is assumed that the structure of the syncarp is homologous.

In *Parartocarpus* the stamens and ovaries are sunken in cavities which are described as receptacular, and have been shown to be separated by walls that are largely if not entirely of intercalary origin. The surface of the receptacle is covered by indurated, spinous, conical or truncate processes that may represent either perianth segments fused basally around the opening of each cavity and solid sterile perianths between these, or secondarily modified interfloral bracts, taking into account the less reduced structure of the related African genus *Treculia*. In *Treculia* perianths are present (tubular in the male, and of linear segments in the female) and are sunken with the stamens and ovaries between the fused stalks of interfloral bracts, the heads of which somewhat resemble the processes in *Parartocarpus*. In both these genera there is a well developed basal involucre. The ovule has been found to be pendulous rather than basal in *Hullettia* and the genus is therefore removed from the Conocephaloideae to the Arto-

carpoideae. The stamens and ovaries are apparently enclosed in cavities as in *Parartocarpus* and there is an involucre of fleshy bracts. It is assumed that the structure of the receptacle is homologous, and that the surface is naked, perianths and interfloral bracts being absent.

The orientation of the embryo and the mode of germination confirm the above alliances. In *Prainea* and *Artocarpus* the embryo is straight (or nearly so) and germination in the latter is hypogeal. In *Parartocarpus* and *Treculia* the embryo is curved, with folded incumbent cotyledons, and germination is epigeal. The embryo of *Hullettia* resembles that of *Parartocarpus* in its orientation but is straight.

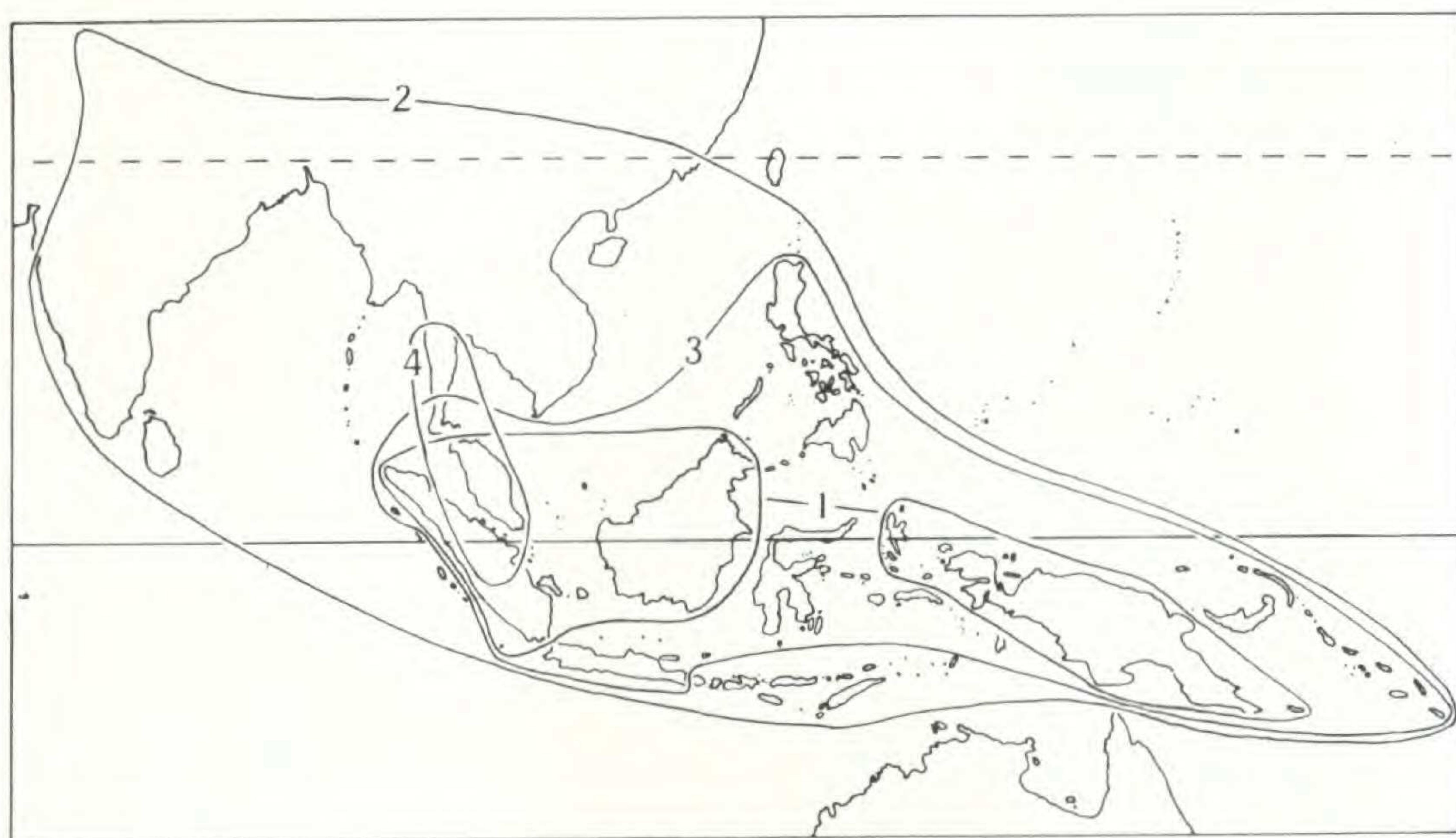


FIG. 9. Distribution of the genera. 1, *Prainea*; 2, *Artocarpus*; 3, *Parartocarpus*; 4, *Hullettia*.

The arrangement of the leaves and stipules serves to distinguish *Parartocarpus* and *Hullettia* from each other, and also from *Prainea* and *Artocarpus*. In the last genus this character readily defines two natural subgenera, *Artocarpus* and *Pseudojaca*, further differentiated by details of the glandular epidermal hairs and the spongy mesophyll which also separate them from *Prainea*. Renner's observations (1907) on leaf anatomy have been expanded and confirmed but his reduction of *Prainea* to the status of a section under *Artocarpus* is not upheld. In vegetative characters the interrelations between the three groups are reticulate, but these indicate the occurrence of parallel evolution and the differences in the female inflorescences override them.

Prainea, *Artocarpus*, *Parartocarpus* and *Hullettia*, together with *Treculia*, form a group of genera united by their condensed capitate inflorescences and large embryos. *Prainea* and *Artocarpus* are closely related to each other, while *Treculia*, *Parartocarpus* and *Hullettia* form a less closely allied series, both groups showing increasing reduction of the inflorescences. Whether these genera together form a natural group within

the Moraceae cannot be certain until an up-to-date revision of the entire family has been carried out, but, from a review of the other Old World genera, it seems probable. The syncarpia of *Artocarpus* and *Parartocarpus* are striking examples of parallel evolution. These two genera and *Hullettia* each represent a highly specialized evolutionary end-point, though reflecting a general tendency for the female inflorescence to become a syncarpium having the ovaries enclosed in either floral or axial tissue.

KEYS TO THE OLD WORLD GENERA OF THE ARTOCARPEAE

NATURAL KEY

1. Inflorescences without an involucre; embryo straight.
 2. Female perianths free, only fruiting perianths enlarging and projecting beyond surface of mature head; leaves alternate and distichous; stipules and scars lateral or partially intrapetiolar; gland-hairs with 4–8-celled head; mesophyll loose, cell-contents resinous. 1. *Prainea*.
 2. Female perianths fused to form a syncarp; entire head enlarging at maturity. 2. *Artocarpus*.
 3. Leaves spirally arranged; stipules amplexicaul, scars annulate; gland-hairs with 4–16-celled head; mesophyll long-armed with globose or ellipsoid resin-cells. Subgenus *Artocarpus*.
 3. Leaves alternate and distichous; stipules and scars lateral or partially intrapetiolar; gland-hairs with 1(–6)-celled head; mesophyll compact, lacking resin-cells. Subgenus *Pseudojaca*.
1. Inflorescences with an involucre of triangular, ovate or orbicular bracts; embryo curved (except *Hullettia*).
 4. Involucre multiseriate; stamens enclosed in tubular perianths, these and ovaries sunken between partially fused interfloral bracts; stipules amplexicaul, scars annulate. (*Treculia*).
 4. Involucre uniseriate; stamens and ovaries sunken in cavities in receptacle; stipules non-amplexicaul, scars not annulate.
 5. Surface of receptacle armoured from indurated, spinous, conical or truncate processes; stipules fused, intrapetiolar, triangular. 3. *Parartocarpus*.
 5. Surface of receptacle not armoured, smooth; stipules paired and lateral, linear. 4. *Hullettia*.

ARTIFICIAL KEY BASED ON VEGETATIVE CHARACTERS

1. Stipules amplexicaul, leaving annulate scars.
 2. Leaves spirally arranged. 2. *Artocarpus* subg. *Artocarpus*.
 2. Leaves, at least on ultimate branches, alternate and distichous. (*Treculia*).
1. Stipules not amplexicaul, scars not annulate.
 3. Leaves spirally arranged.
 4. Stipules paired, linear, scars lateral, round; leaves minutely punctate beneath. 4. *Hullettia*.
 4. Stipules fused, intrapetiolar, scars elongate; leaves not as above. 3. *Parartocarpus*.
 3. Leaves alternate and distichous.
 5. Leaves abruptly and distinctly acuminate, glabrous; gland-hairs sunken, head 4–8-celled; mesophyll loose, cell contents resinous. 1. *Prainea*.

5. Leaves usually not abruptly acuminate, often pubescent; gland-hairs not sunken, head 1(-6)-celled; mesophyll compact, without resin.

..... 2. *Artocarpus* subg. *Pseudojaca*.

NOTES ON THE TAXONOMIC TREATMENTS

KEYS. These are intended to indicate, as far as is practicable, the natural affinities of the species and to enable the identification of most material bearing either male or female inflorescences and, where possible, of sterile specimens. Distinguishing characters for sterile material of species with overlapping areas of distribution have been given in the notes under the species.

TYPES. These have been listed, where known, at the end of the references for each accepted name and synonym. All these specimens have been examined unless otherwise stated. Detailed localities have been given here only when the type or a duplicate has not been seen, since they otherwise appear in the lists of specimens. Lectotypes have been selected for most species where the original description gave syntypes and for those species where the holotype has been destroyed, but isotypes exist. Neotypes have only been chosen, where necessary, for accepted names.

SPECIFIC DESCRIPTIONS. These have been prepared from herbarium material, with the addition of details from field notes. The inflorescences have been described from material preserved in alcohol when this has been available. Otherwise the male flowers have been described from material boiled up in water. Where measurements in published descriptions differ greatly from those found in the specimens seen they have been given, together with the source. Measurements of the female inflorescences are probably frequently too small, since fully ripe fruits are not often collected, and many of the species will certainly have larger sapling leaves than indicated here. Descriptions of new species have been prepared from the types and supplemented by details from other collections enclosed in brackets.

Details of the stipules have only been given for *Artocarpus* subg. *Artocarpus*, *Parartocarpus* and *Hullettia*, since in the other groups they do not show significant variation between the species. For the same reason, details of the glands on the leaves and of the presence or absence of a hypodermis have only been given for *Artocarpus* subg. *Artocarpus*. In describing the leaves the term "main veins" includes the midrib and the lateral veins, while the term "reticulum" includes the intercostals unless these have been mentioned separately. In counting the lateral veins all those at the base have been included as well as all those clearly distinguishable at the apex.

The inflorescences have been described as immature before anthesis and the female inflorescence has been described as submature between anthesis and maturity. In *Prainea* and *Artocarpus* the interfloral bracts (as opposed to the involucre bracts of *Parartocarpus* and *Hullettia*) are referred to as bracts in the descriptions. In describing the syncarp of *Artocarpus* and *Parartocarpus* the variously shaped projections of the

surface, excluding peltate interfloral bracts, are referred to as processes or papillae. The morphological nature of these, which has already been discussed, differs both within *Artocarpus* and between *Artocarpus* and *Parartocarpus*. The terms "core" and "wall" refer respectively to the receptacle and the surface layer formed by the fused perianths.

CITATION OF SPECIMENS. These have been listed by areas, arranged from west to east in continental Asia (excluding Malaya) and according to the enumeration of geographical units by van Steenis (1950) in Malaysia, except that in the latter the order of the first four units has been changed to Malaya, Sumatra, Borneo, Java, in order to reflect the geographical continuity of Malaya with Asia and the close connection of Borneo with Malaya and Sumatra. In the Philippine Islands, Luzon and Mindanao have been further subdivided into provinces, and specimens from eastern New Guinea have also been listed according to recent political subdivisions.

The herbaria in which the collections have been seen are indicated by the abbreviations of the Index Herbariorum, Part I. ed. 3. 1956. These have been given above in conjunction with the acknowledgements. In addition, the following abbreviations may be noted which have been used preceding the collection numbers.

- bb — Bossen buitengewesten; i.e., collections made by the Netherlands Indies Forest Service from areas outside Java.
- BS — Bureau of Science, Manila, Philippines.
- CF — Conservator of Forests series, Forest Institute, Kepong, Malaya.
- FB — Forestry Bureau, Manila, Philippines.
- NIFS — Netherlands Indies Forest Service; this has been prefixed to those collections made by the service which do not have bb numbers. (They are numbered in several series, distinguished by various abbreviations indicating where they were collected.)
- PB — Piante Bornensi; collected by Beccari.
- PP — Piante Papuane; collected by Beccari.
- SB — Species Blancoanae; collected by Merrill to illustrate his book of that title.
- SFN — Singapore field number.

Localities have been cited as given on the original label, apart from some minor corrections. Where important alterations have been necessary, these have been added in brackets. The Dutch *oe* has been transliterated throughout as *u*. The presence of male and female inflorescences has been indicated, but in *Prainea*, *Parartocarpus* and *Hullettia* the sex of immature inflorescences can often be determined only by dissection, and these have been recorded as "infl."

VERNACULAR NAMES. Only those names have been cited which are of fairly common occurrence for a given species, or which are of particular interest. The following names are applied to any species of *Artocarpus* subg. *Pseudojaca*: *Chay* or *Cay chay* (Annamite), *Kwai muk* or *Hung kwai muk* (China), *Tampang* (Malay), and *Cubi* and *Anubing* (Philippines). The name *Tampang* is also applied to *Prainea limpato*. In *Artocarpus* subg. *Artocarpus*, *Terap* is the Malay name for *A. odoratissimus*, *A. scorte-*

chinii, *A. elasticus*, *A. sericicarpus* and *A. tamaran*. Many other species of this subgenus are distinguished by their own names, which are usually accurately applied.

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STUDIES IN ARTOCARPUS AND ALLIED GENERA. II.
A REVISION OF PRAINEA

FRANCES M. JARRETT

Prainea King in Hook. f. Fl. Brit. Ind. 5: 546. 1888; King, Ann. Bot. Gard. Calcutta 5(2): 162. *t.* 196. 1896; Engler & Prantl, Nat. Pflanzenfam. Nachträge II–IV. 122. 1897; Boerl. Handl. Fl. Ned. Ind. 3: 337, 372. 1900; Becc. For. Borneo 635. 1902, Webbia 5: 563. 1923; Ridley, Fl. Malay Penin. 3: 358. 1924; Van Steenis, Bull. Jard. Bot. Buitenzorg III. 12: 259. 1932; Jarrett, Jour. Arnold Arb. 40: 8, 11. *fig.* 1, *a–c*, *fig.* 3, *a–c*. 1959. TYPE SPECIES: *Prainea scandens* King. *Artocarpus* section *Prainea* Renner, Bot. Jahrb. 39: 366. 1907.

Trees (? or climbers). *Leaves* alternate and distichous, simple, entire, penninerved, glabrous; epidermal gland-hairs sunken, heads globose, 4–8-celled; spongy mesophyll loose, cell contents somewhat resinous; juvenile leaves elongate. *Stipules* paired, small (to 5 mm. long), lateral or intra-petiolar, scars non-amplexicaul.

Inflorescences unisexual, capitate, heads globose, or the male short-obovoid, pedunculate, solitary or paired in leaf-axils; flowers mixed with numerous narrowly peltate, clavate or spatulate interfloral bracts; perianths free, enclosing a single stamen or ovary; involucre absent. *At anthesis* perianths and bracts compactly covering surface; *male head* with numerous flowers; perianths tubular, bilobed or perforate above; stamens shortly exerted; *female head* with fewer flowers (c. 20–100); perianths tubular, clavate, fleshy above, the mouth contracted, very shortly 2–4-lobed or merely perforate; ovary unilocular, style apical, bifid, the branches exerted, ovule subapical. *Mature female head* with 1–20 flowers forming fruit, perianths greatly enlarged and projecting from surface, fleshy, subglobose to ellipsoid; remaining perianths elongating somewhat or not at all and surface hence loose or compact; mature ovary membranous, style apical, seed large, attached laterally near base, testa absorbed except the thickened saucer-shaped basal portion, endosperm none, embryo straight, longitudinal, cotyledons equal, appressed faces oblique to median plane of ovary, radicle and plumule minute, apical; interfloral bracts persistent.

DISTRIBUTION: Malaya, Sumatra, Borneo, Moluccas, New Guinea.

The genus *Prainea*, described by King in 1888, was based on a single species from Malaya, *P. scandens*, which he illustrated in 1896 in "A Century of New and Rare Indian Plants." King described the ovule as basal and hence placed the genus incorrectly in the Conocephaloideae. However, although the mature seed is attached sub-basally (in *P. papuana*, the only species of which adequate material has been available for study),

if the ovary is examined at anthesis the position of the ovule is found to be lateral just below the apex of the loculus.

In 1902 Beccari, in the appendix to "Nelle Foreste di Borneo" entitled "Nuove Specie di *Artocarpeae* Malesi e Papuane," briefly discussed the inflorescences of *Prainea*, stating that he had found the ovule to be pendulous [at anthesis] in spirit material of his *P. cuspidata* (= *P. limpato*) and that the genus was allied to *Artocarpus*, differing only in the structure of the female inflorescence. He also questioned King's description of *Prainea scandens* as a climber. He described as new the three other species of *Prainea* here recognized and a fourth which was an identification of Rumphius' *Metrosideros spuria* (= *Artocarpus fretissii* Teysmann & Binnendijk).

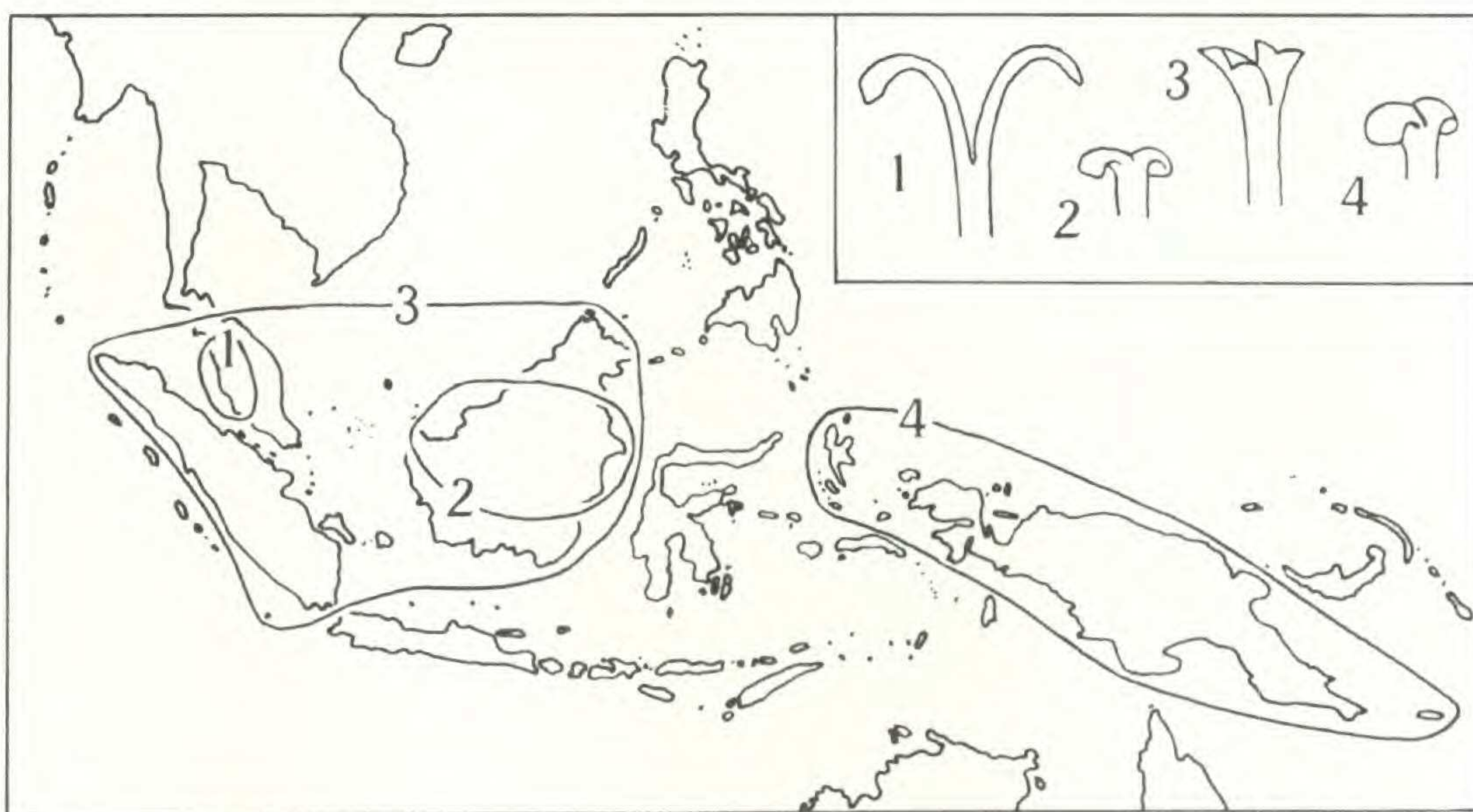


FIG. 10. Distribution of the species of *Prainea*, with inset showing styles; 1, *P. scandens*; 2, *P. frutescens*; 3, *P. limpato*; 4, *P. papuana*.

Renner's reduction of the genus in 1907 to the status of a section under *Artocarpus* has been discussed fully in the introductory paper of this series and rejected on the grounds that the resemblance in leaf structure to subg. *Artocarpus* and in leaf and stipular arrangement to subg. *Pseudojaca* is of less significance than the difference between the free perianths of the female inflorescence of *Prainea* and the syncarpium of *Artocarpus*. In uniting *Prainea* with *Artocarpus*, Renner correctly identified Beccari's *Prainea cuspidata* with Miquel's *Artocarpus limpato* (1861) and listed four species which are equivalent to those recognized here. He found the ovule to be pendulous in *Prainea frutescens* and thus the only species in which this character has not been established is *P. scandens*.

The species are readily separable and the characters used may be seen from the key. No marked variation occurs within the genus, although *P. scandens* and *P. frutescens*, on the one hand, and *P. limpato* and *P. papuana*, on the other, are somewhat more closely allied to each other by leaf characters and the length of the peduncle.

The genus *Prainea* is entirely restricted to Malaysia, with three species in western Malaysia, of which one is endemic to Malaya, and another to Borneo, and a single species in the Moluccas and New Guinea. Van Steenis, in discussing the distribution of the Styracaceae in 1932, cited *Prainea* as an example of a genus which, like that family, occurs in both the western and the eastern parts of Malaysia, but not in the Philippines. The absence of *Prainea* from the Philippines has been confirmed thus far and, moreover, the genus is apparently lacking from nearly all of the geologically unstable area between the Sunda and Sahul continental shelves. Species of *Artocarpus* showing a similar pattern of distribution will be noted in a discussion of the geographical distribution of this group of genera at the conclusion of this series of papers.

KEY TO THE SPECIES OF PRAINEA

1. Male peduncles 5–15 mm.; female peduncles 10–25 mm.; twigs c. 1.5 mm. thick; leaves with 6–12 pairs lateral veins.
 2. Male heads to c. 15 mm. across; female heads to c. 35 mm. across with fruiting perianths projecting up to 25 mm.; stylar branches 2 mm. long, acute. 1. *P. scandens*.
 2. Male heads 4–6 mm. across; female heads to c. 10 mm. across with fruiting perianths projecting less than 10 mm.; stylar branches 0.5 mm. long, truncate. 2. *P. frutescens*.
1. Male peduncles 15–60 mm.; female peduncles 35–110 mm.; twigs 2–5 mm. thick; leaves with 9–24 pairs lateral veins.
 3. Male heads to c. 15 mm. across; female heads to c. 35 mm. across with fruiting perianths projecting up to 15 mm.; stylar branches forked; mature leaves with lateral veins distinctly prominent beneath, areolae bullate above only, or not at all. 3. *P. limpato*.
 3. Male heads 3–8 mm. across; female heads to 20 mm. across with fruiting perianths projecting up to 10 mm.; stylar branches obtuse; mature leaves with lateral veins not or shallowly prominent beneath, areolae often bullate on both surfaces. 4. *P. papuana*.

1. *Prainea scandens* King in Hook. f. Fl. Brit. Ind. 5: 547. 1888; King, Ann. Bot. Gard. Calcutta 5(2): 162. *t.* 196. 1896; Ridley, Fl. Malay Penin. 3: 358. 1924. Syntypes, Malaya, *King* 3549, 3693 (CAL, not seen); duplicates examined (BM, K).

Artocarpus scandens Renner, Bot. Jahrb. 39: 367. 1907.

Climber(?), height to 20 m. *Twigs* c. 1.5 mm. thick, finely rugose, minutely appressed pubescent, soon glabrescent. *Leaves* 9–17 × 3.5–7 cm., obovate-elliptic, varying elliptic or oblong-elliptic, abruptly contracted into a narrow acumen to 1.5 cm. long, base cuneate, margin entire; midrib prominent beneath, lateral veins slightly so; lateral veins 9–12 pairs, curved, inarching at margin, often with secondary loops; intercostals not parallel; glabrous, dark green, drying greenish above, pale to reddish brown beneath, petiole 5–15 mm. long.

Inflorescences solitary in leaf-axils. *Male head* (not at anthesis) to 15 mm. across, short-obovoid; perianths tubular, bilobed above, 1 mm. long; stamen immature, filament cylindric, anther oblong, 0.3 mm. long; bracts slenderly stalked, heads peltate, 0.4 mm. across; peduncle to 15×1.5 mm., velutinous; *female head* at anthesis with bifid styles exerted, branches 2×0.2 mm., acute. *Mature female head* to 35 mm. across (excluding fruiting perianths), globose, loosely covered by numerous flowers and bracts, yellow, drying brown; fruiting perianths 1–7, projecting to 25 mm., ellipsoid, 15 mm. across, broadly and obtusely attenuate; remaining perianths 12–15 mm. long, apices clavate, perforate, minutely pubescent, 0.8 mm. across; bracts numerous, slenderly stalked, heads clavate, 0.8 mm. across, pubescent; peduncle $20\text{--}25 \times 2.5$ mm., puberulent.

DISTRIBUTION: in lowland evergreen forest to 2500 ft., endemic to Malaya.

Malaya. PERAK: Larut, *King* 3549, Nov. 1882 (BM, K, ♂), *King* 3693 Dec. 1882 (BM, K, ♀). SELANGOR: bridge where Gap road crosses Sungei Semangko, *Strugnell Kepong FN* 49703 (SING, ♀, detached inflorescence with leaves of *Artocarpus rigidus*).

The material of this species is inadequate, but King's collections agree well on vegetative characters and the mature female head on *Strugnell Kepong FN* 49703 matches that of *King* 3693.

This species appears to differ from all others in *Prainea* and *Artocarpus* in being a climber instead of a tree. The labels on both King's collections describe the plants as "creepers." *King* 3693 originally read "a tree with slender hanging branches 50–60 ft. high . . . clinging to another tree" and was altered later.

2. *Prainea frutescens* Becc. For. Borneo 635. 1902. Holotype, Borneo, *Beccari PB* 667 (FI); isotypes (FI, K, P).

Parartocarpus sp. Benth. & Hook. f. Gen. Pl. 3: 375. 1880.

Artocarpus frutescens Renner, Bot. Jahrb. 39: 367. 1907.

Trees, height to 30 m. *Twigs* c. 1.5 mm. thick, finely and acutely rugose, appressed puberulent, soon glabrescent. *Leaves* $5\text{--}16 \times 3\text{--}7$ cm., obovate-elliptic to obovate- or elliptic-oblong or elliptic, abruptly contracted into a narrow acumen to 2 cm. long, base cuneate, rarely oblique with one side rounded, margin entire; midrib prominent beneath, lateral veins slightly so; lateral veins 6–10 pairs, curved, inarching at margin; intercostals not parallel; glabrous, drying greenish to pale or reddish brown; petiole 7–12 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis: male head* 4–6 mm. across, subglobose to short-obovoid; perianths tubular, 0.8 mm. long, minutely pubescent; stamen 1.2 mm. long, filament cylindric, anther oblong, 0.15 mm. long; bracts slenderly stalked, heads peltate, 0.3 mm. across, ciliate; peduncle $5\text{--}12 \times 1$ mm., velutinous; *female head* with

bifid styles exserted, branches 0.6×0.2 mm., truncate. *Mature female head* to 10 mm. across (excluding fruiting perianths), globose, compactly covered by 20–30 flowers and numerous bracts; fruiting perianths 2 (in only mature head seen) projecting to 7 mm., ovoid, 6 mm. across, obtuse; remaining perianths c. 2.5 mm. long, apices obtuse, minutely pubescent, 1.5 mm. across, mouth shortly bilobed; bracts coherent in groups, slenderly stalked, heads narrowly peltate, 0.25 mm. across, pubescent; peduncle $13\text{--}16 \times 1.5$ mm., short-pubescent.

DISTRIBUTION: in lowland evergreen forest to 200 ft., endemic to Borneo.

Borneo. SARAWAK: near Kuching, *Beccari PB 667*, Nov. 1865 (FI, K, P. ♂, ♀), *Haviland 3111* (BM, BO, ♀). EAST AND NORTHEAST BORNEO. W. Kutei: *bb 16183* (A, BO); Longbleh, Sungei Pekan, *bb 29606* (A, BO, L, SING, ♂); Mujup, *bb 16785*, *bb 16911* (A, BO, L).

3. *Prainea limpato* (Miq.) Beumée ex Heyne, Nutt. Pl. Ned.-Ind. ed. 2. 1: 579. 1927.

Artocarpus limpato Miq. Fl. Ind. Bat. Suppl. 421. 1861; Renner, Bot. Jahrb. 39: 367. 1907. Syntypes, Sumatra, *Diepenhorst HB 2092*, *HB 2500* (U); lectotype, *Diepenhorst HB 2092* (U).

Urostigma diepenhorstii Miq. Fl. Ind. Bat. Suppl. 439. 1861. Holotype, Sumatra, *Teysmann HB 716* (U); isotype (BO).

Ficus diepenhorstii (Miq.) King, Ann. Bot. Gard. Calcutta 1: 181. 1888.

Prainea cuspidata Becc. For. Borneo 636. 1902. Holotype, Borneo, *Beccari PB 2825* (FI); isotypes (FI, K, P).

Prainea multinervia Merr. Philip. Jour. Sci. 29: 364. 1926, Pl. Elmer. Born. 46. 1929. Holotype, Borneo, *Castro and Melegrito 1610* (UC, not seen); isotypes (A, BO, K).

Trees, height to 30 m. (60 m. fide *Gusdorf 115*), buttressed, bark dark red-brown, peeling off in flakes. *Twigs* 2–5 mm. thick, finely rugose, appressed puberulent, soon glabrescent. *Leaves* $10\text{--}33 \times 4\text{--}13$ cm., oblong, varying oblong- or obovate-elliptic, or elliptic, apex abruptly contracted or often subtruncate below a narrow acumen to 1.5 cm. long, base cuneate, or often oblique with one side subcordate, margin entire; midrib and lateral veins prominent beneath, intercostals slightly so, areolae often slightly bullate above; lateral veins 11–24 pairs, straight or slightly curved, inarching at margin conspicuous; intercostals forming rectangular net; glabrous, drying dark to pale reddish brown; petiole 8–22 mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis: male head* c. 15 mm. across, globose; perianths tubular, perforate, 1.4 mm. long, minutely pubescent; stamen 1.8 mm. long, filament cylindric, anther oblong, 0.4 mm. long; bracts slenderly stalked, heads peltate, 0.3 mm. across, ciliate; peduncle $30\text{--}40 \times 2$ mm., glabrous to short-pubescent; *female head* with bifid styles exserted, branches 0.5×0.2 mm., forked at the tips. *Mature female head* to 35 mm. across (to 55 mm. including fruiting perianths), globose, loosely covered by numerous flowers and bracts, yellow-green, drying brown; fruiting perianths 8–20, projecting to

15 mm., ellipsoid, 10 mm. across, obtuse or broadly and obtusely attenuate; remaining perianths c. 4 mm. long, apices clavate, perforate, minutely pubescent, 1.5 mm. across; bracts slenderly stalked, heads spathulate, 0.3 mm. across, ciliate; peduncle $75-110 \times 2-3$ mm., puberulent.

VERNACULAR NAMES: *Tampang* (Malay), Sumatra, Borneo; *Limpato*, Sumatra.

DISTRIBUTION: in lowland evergreen forest to 1700 ft., Malaya, Sumatra, Borneo.

Malaya. KEDAH: Weng road, near Baling, *Best SFN 21266* (K, SING, infl.). Sumatra. ATJEH: Bivak Aer Putih, waterfall near Pendeng, Gajolanden. *Van Steenis 9270* (BO, L, ♀). WEST COAST: Fort Elout, *Teysmann HB 716* (BO, U); Priaman, *Diepenhorst HB 2092* (BO, L, U, ♀), *HB 2500* (BO, L, U, ♂), *HB 2914* (BO). INDRAGIRI: Batang Peranap, *bb 30095* (BO, L); Muara Serangge, *bb 30066* (BO, L); Peranap, *bb 30105* (A, BO, L). DJAMBI: Danau Lama, *bb 13639* (BO). PALEMBANG: Lematang Ilir, Gunong Megang, *NIFS T 340* (BO, L ♂), *NIFS T 521* (BO, K, L, U, ♀); Lematang Ilir, Semangus, *bb 32063* (A, BO, L, SING, ♂), *bb 32085* (A, BO, L, SING); Mulak Ulu, *Grashoff 323* (BO, L). LAMPONGS: Manggala, *Gusdorf 115* (BO, ♀). ENGGANO: forest near Bua bua, *Lutjeharms 4558* (A, BO, K, L, P, SING). Borneo. SARAWAK: Gunong Braam, near Sabungo, *Beccari PB 2825*, Nov. 1866 (FI, K, P, ♂, ♀). SOUTH AND SOUTHEAST BORNEO: Tanah Bumbu, Kampong Baru, *bb 13364* (BO). EAST AND NORTHEAST BORNEO: Berouw, Domaring, *bb 18817* (A, BO, L); Bulungan, Mara, *bb 10809* (BO); Upper Mahakam, D. Parei, *bb 20743* (A, BO, L). BRITISH NORTH BORNEO: Limanis, *Wood 1790* (BO, ♂); Tawao, Elphinstone Prov., *Elmer 21799* (A, BM, BO, GH, K, L, P, SING, U, ♀). BANGUEY ISLAND: *Castro & Melegrito 1610*, July-Sep. 1923 (BO, K, ♂).

The appearance of the mature female head is rather variable, owing to differences in the number of fruiting perianths and in the extent to which the other perianths elongate after anthesis. The leaf form in which the apex is subtruncate below the acumen is distinctive and is found only in this species of the genus.

4. *Prainea papuana* Becc. For. Borneo 635. 1902. Holotype. New Guinea, *Beccari PP 675* (FI); isotypes (FI).

Artocarpus papuanus Renner, Bot. Jahrb. 39: 367. 1907, non Diels. 1936.

Prainea microcephala J. J. Smith, Bull. Jard. Bot. Buitenzorg III. 6: 80. 1922. Syntypes, Ternate, *Beguin 691*, Halmaheira, *Beguin 1919*, 1980. 2242 (BO); lectotype, *Beguin 1980* (BO).

Parartocarpus papuanus S. Moore, Jour. Bot. 61 Suppl. 52. 1923, non Becc. 1902; Diels, Bot. Jahrb. 67: 175. 1936. Syntypes, New Guinea, *Forbes 331*, 411 (BM); lectotype, *Forbes 411* (BM).

Trees, height to 35 m., bark brown, peeling off in flakes. Twigs 2-3 mm. in diameter, finely rugose, appressed puberulent, soon glabrescent. Leaves $8-26 \times 4-12$ cm., oblong, varying elliptic, abruptly narrowed into an acumen to 1.5 cm. long, base cuneate or rounded, often oblique with one side subcordate, margin entire; midrib prominent beneath, lateral veins

slightly so, areolae often bullate on both surfaces; lateral veins 9–20 pairs, straight or slightly curved, inarching at margin conspicuous; intercostals not parallel; glabrous, drying red-brown, grey or green above, dark to pale brown beneath; petiole 8–18 mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis: male head* 3–8 mm. across, globose; perianths tubular, clavate, shortly bilobed above, 1.8 mm. long, minutely pubescent; stamen 2.5 mm. long, filament slender, cylindric, anther oblong, 0.4 mm. long; bracts slenderly stalked, heads clavate, 0.4 mm. across; peduncle $15\text{--}60 \times 2$ mm., velutinous; *female head* olive green, with bifid styles exerted, branches 0.7×0.5 mm., obtuse. *Mature female head* 10–20 mm. across (excluding fruiting perianths), globose, loosely to compactly covered by c. 25–100 flowers and numerous bracts, orange, drying brown; fruiting perianths 2–12(–25), projecting to 10 mm., subglobose to conical, 10 mm. across, mucronate; remaining perianths c. 2.5×1 mm., clavate, mouth contracted, obtusely 4-lobed; bracts slenderly stalked, heads clavate, 0.5 mm. across, often coherent in groups; peduncle $30\text{--}90 \times 2$ mm., velutinous.

DISTRIBUTION: in lowland evergreen forest to 3500 ft., Moluccas (Halmaheira group), New Guinea.

Moluccas. MOROTAI: Gunong Moku, *Anang* 263 (L); Mt. Permatang, along the Sangowo River, *Kostermans* 959 (L, SING); Tjaw, *Kostermans* 836, 837 (L). HALMAHEIRA: Galela, Soa Tobaru, *Beguin* 1919, Dec. 1921 (BO, K, L, U, ♀), 1926 (BO, L, ♀), 1980, May 1922 (BO, L, P, SING, U, ♀); Kampong Toliwang, *Idjan/Moehtar* 364 (K); W. Pitu, *Beguin* 2242, Nov. 1922 (BO, K, L, P, U). TERNATE: Laguna, *Beguin* 691, May 1920 (BO, L, ♀). BATJAN: Masurung, *bb* 23133 (BO, L).

New Guinea. VOGELKOP: Andai, *Beccari PP* 675, 1872 (FI, ♂, ♀); Manokwari, Pomi, Kolonisatie, *bb* 15897 (BO, ♀); n. of Ransiki, 80 km. s. of Manokwari, *Kostermans* 4746 (A, K, L, SING, ♀); Sorong, *Beccari s.n.* (FI). DUTCH NORTH NEW GUINEA: Bernhard Camp, Idenburg River, *Brass & Versteegh* 13167, 14122 (A, ♀). PAPUA. Central Division: Boridi, *Carr* 14976 (SING, ♀); Koitaki, *Carr* 12213 (BM, K, L, SING, infl.), 12586 (BM, K, SING, infl.), 12886 (BM, K, L, SING, ♀); Sogeri, *Forbes* 331, 411, 1885–6 (BM, K, L, ♀). Milne Bay District, Cape Vogel Peninsula: near Medino village on n. coast, *Hoogland* 4666 (A, ♀); Menapi, *Brass* 22000 (A, ♀). MANDATED TERRITORY OF NEW GUINEA. Morobe District: *Womersley NGF* 2994 (A, BO K, L, ♀); Quembung, Sattelberg, *Clemens* 8099 (A, ♀). D'ENTRECASTEAUX Is. Normanby I.: Lebudowa River, *Brass* 25517 (K, L, ♀); Waikaiuna Bay, *Womersley & Brass NGF* 8674 (A, K, ♀); near Waikaiuna Plantation, *Jackson NGF* 4109 (A, K, L, SING, ♀). JAPEN: Serui, *bb* 30434 (BO, L), *bb* 30655 (L). LOUISIADE ARCHIP.: Misima I., Mt. Sisa, *Brass* 27523 (K, L, ♀).

In his description of *Parartocarpus papuana*, S. Moore cited a third specimen, *Forbes* 503, but this has not been found either at the British Museum (Natural History) or elsewhere.

The female head in *Prainea papuana* shows a variability similar to that of *P. limpato* in the number of seeds formed and in the degree of elongation of the perianths after anthesis. The latter is partially correlated with

a geographical variation in the diameter of the head at anthesis. In eastern New Guinea the female head then has a diameter of 10–15 mm. and the surface generally remains compact at maturity, but in the Vogelkop and the Moluccas the diameter is only about 5 mm. at anthesis and later all the flowers usually elongate somewhat so that at maturity the surface becomes loose. A parallel variation occurs in the size of the male head. However, the collections from Dutch North New Guinea are intermediate, with a diameter of 8–10 mm. at anthesis and with the surface remaining fairly compact. The creation of subspecies is therefore not regarded as justifiable.

SPECIES EXCLUDENDA

Prainea rumphiana Becc. For. Borneo 636. 1902 = *Artocarpus fretissii* Teysm. & Binnend. Abh. Naturf. Ges. Halle 9: 189. 1866.